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Dynamics of grassland plant diversity in changing landscapes

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications, which are denoted in the text by the Roman numerals:

I Saar L., de Bello F., Pärtel M., & Helm, A. (2017) Trait assembly in grasslands depends on habitat history and spatial scale. *Oecologia*, **184**, 1–12.

II Saar, L., Takkis, K., Pärtel, M., & Helm, A. (2012) Which plant traits predict species loss in calcareous grasslands with extinction debt? *Diversity and Distributions*, **18**, 808–817.

III Kasari L., Saar L., Bello F., Takkis K., & Helm A. (2016) Hybrid ecosystems can contribute to local biodiversity conservation. *Biodiversity and Conservation*, **25**, 3023–3041.

IV Saar, L., Takkis, K., Laanisto, L., Carmona, C.P., Kasari, L., Hallikma, T., Pärtel, M., & Helm, A. Losers and winners in European grasslands: a functional analysis of temporal trends of vascular plants – *manuscript*

Author's contribution to the publications:

I had the main responsibility in analysing the data and preparing the manuscript

II participated in developing the idea and data collection, had the main responsibility in analysing the data and preparing the manuscript

III contributing in developing the idea, participating in data collection, participated in manuscript preparation

IV participated in developing the idea, had the main responsibility in collecting and analysing data and preparing the manuscript

1. INTRODUCTION

1.1. Theoretical background

Mitigating and reversing human-induced biodiversity loss is one of the main challenges that humanity faces (Balmford et al., 2005; Pereira et al., 2012; Johnson et al., 2017). The conversion of natural and semi-natural habitats to agricultural land, plantations or urban areas, the cessation of traditional management activities, nitrogen deposition and fertilization are some examples of human-induced effects that have considerably influenced biodiversity in many landscapes over the past century (Bobbink et al., 1998; 2010; Sala et al., 2000; Van Calster et al., 2008). For example, the area of historically widespread semi-natural grasslands has declined in many regions of Europe by up to 97% compared to their historical coverage (Adriaens et al., 2006; Dengler et al., 2014; Ridding et al., 2015). The majority of European semi-natural and natural grasslands are nowadays highly fragmented and degraded (Pärtel et al., 2005; Habel et al., 2013; Dengler et al., 2014). Evidently, populations will deteriorate and go locally and regionally extinct when their habitats have declined or completely vanished (Hanski, 2011). In order to mitigate the effects of global change on semi-natural habitats, we need knowledge-based actions. Reducing and reversing the effects of decreased habitat area and quality on biodiversity and avoiding losses of important ecosystem functions and services needs concerted input by scientists, conservationists, policy-makers and the whole society (Díaz et al. 2007; Suding et al. 2008; Cardinale et al. 2012).

Species local extinction or decreased abundance in relation to grassland area loss and degradation has been detected in many studies (Fischer & Stöcklin, 1997; Walker & Preston, 2006; Wesche et al., 2012). However, due to slow intrinsic population dynamics, species response to changed environmental conditions can often be delayed, and eventual species extinction from fragmented landscapes can proceed after several decades or more (Hanski & Ovaskainen, 2002; Piqueray et al., 2011; Bagaria et al., 2015). This phenomenon, known as extinction debt (i.e. the future extinction of species due to events occurred in the past), hampers our ability to fully understand the complete effects of fragmentation and decreased habitat quality on biodiversity (Tilman et al., 1994; Helm et al., 2006; Jackson & Sax, 2010). Extinction debt has been detected for different organisms, particularly for habitat specialists, i.e. species that are typical to a given community and belong to its historically developed habitat-specific species pool (Kuussaari et al., 2009; Krauss et al., 2010; Sang et al., 2010). For example, Helm et al. (2006) detected the occurrence of extinction debt in calcareous grasslands in Estonia that have lost more than 70% of their habitat area since the 1930s. These grasslands are expected to lose ca 40% of their habitat specialist species in the future due to the habitat loss that has already occurred. Extinction debt is thus a threat, but at the same time, also an opportunity for biodiversity conservation. The delayed response of populations can give us

additional time to develop and implement proper conservation and restoration measures (Kuussaari et al., 2009).

Whether species richness decreases or increases at local and regional scales following habitat loss and degradation is determined by the balance between extinction and colonization events (Jackson & Sax, 2010). Despite the decreased number and abundance of species characteristic to semi-natural grasslands, total species richness has often increased temporarily following the cessation of traditional habitat management (Bagaria et al., 2015). Besides a number of grassland species that decline or disappear when traditional management ceases, there are also species that benefit from altered conditions. Species better suited to the new environmental conditions complement the existing communities and/or replace the locally extinct species, changing community composition (Supp & Ernest, 2014; McCune & Vellend, 2015). Habitats with altered conditions have been shown to be more vulnerable to colonisations of exotic and invasive species, as well to native species from other habitats, i.e. native invasive species (Valéry et al., 2009; Jackson & Sax 2010). Altered environmental conditions, declining habitat area and increasing isolation also result in decreased habitat integrity (i.e. how similar the habitat is to its historical state before extensive area and/or quality loss) and conservation value of grasslands (Helm et al., 2015).

In addition to taxonomical changes in community composition, several studies have reported changes in the functional structure of communities in response to land-use changes (Garnier et al. 2007). Individual species response to habitat change depends largely on their functional traits, habitat preferences and niche requirements (Fischer & Stöcklin, 1997; Piqueray et al., 2011; Supp & Ernest, 2014). Functional traits (morphological, physiological, structural, phenological or behavioral characteristics of organisms that influence species fitness; Nock et al., 2001) describe the adaptation of species to the environment and they can be highly useful for assessing the effects of habitat loss and altered conditions on biodiversity (Louault et al., 2005; Pakeman et al., 2009). Habitat loss and fragmentation modify the spatial structure of populations, but also the physical structure of the environment of remnant habitat patches (Hanski et al., 2011). Thus, functional characteristics related to dispersal and local persistence play the key role in fragmented or deteriorated landscapes, determining which species tolerate changed conditions, and which do not (Kolb & Diekmann, 2005; Tremlová & Münzbergová, 2007; Marini et al., 2012). With increasing eutrophication in European grasslands and the cessation of traditional management, species with better competitive abilities are often suggested to be less prone to extinction following land use changes compared to stress tolerating species adapted to less fertile and regularly disturbed (i.e. mown or grazed) habitats (Walker & Preston, 2006). At the same time, an enhanced dispersal ability of species is suggested to contribute to species survival in fragmented habitats due to the ability to move between fragmented habitat patches (Eriksson & Jakobsson, 1999; Ozinga et al., 2004). However, due to the trade-off between competitive and dispersal ability, good dispersal capacity can instead increase the likelihood of the extinction of species in low-quality habitats (Kneitel &

Chase, 2004). Additionally, studies have also shown that in very isolated habitats, species with good dispersal ability can be hindered due to a higher probability to disperse in the hostile environment (Purschke et al., 2012; Lindborg et al., 2012; Neuenkamp et al., 2016). However, published results on the effect of fragmentation or landscape context on biodiversity dynamics diverge (Cousins, 2009). Despite intensive research, it remains a challenge to predict the responses of particular species and communities under habitat change (Suding et al., 2008) and more knowledge-based approaches are needed.

In addition to individual species responses, an important aspect in conservation and restoration ecology is to understand which mechanisms drive species assembly in communities (Török & Helm, 2017). Functional trait composition and trait values (e.g. community weighted mean values of functional traits) of co-occurring species can be used effectively for detecting the main mechanisms and processes driving species assembly following land-use changes (Cornwell et al., 2006; Adler et al., 2010; de Bello et al., 2012). Co-existing species can be functionally more different than expected by chance (i.e. functional divergence) or more similar (i.e. functional convergence) (Grime, 2006). Functional divergence in communities is an indication of the dominance of biotic effects, such as competition for limiting resources, such as light and nutrients in determining species assembly (i.e. limiting similarity; MacArthur & Levins 1967). Functional convergence indicates that environmental filtering, weaker competitor exclusion or dispersal limitation are the primary mechanisms determining community assembly (Grime, 2006; de Bello et al., 2012). In addition to general trait patterns, individual functional traits can be important for certain assembly processes. For example, resource-related functional traits are generally expected to be linked to abiotic processes, competition-related traits to biotic processes, and regeneration and diaspore traits to dispersal processes (Grime, 2006; Marteinsdóttir & Eriksson, 2014).

Historical land-use parameters (i.e. habitat continuity, historical management intensity and habitat age) have been suggested to control greatly species composition and functional structure in grassland habitats (Aavik et al., 2008; Krause & Culmsee, 2013; Vandewalle et al., 2014). Irrespective of the numerous published studies focussing on habitat history on taxonomic and functional composition of communities, results often vary across different spatial scales, species pool sizes, habitat types or across studied traits (e.g. Cornwell et al., 2006; Adler et al., 2010; de Bello et al., 2013) and still less is known how assembly mechanisms vary in dynamic landscapes subjected to changes in land-use.

In order to estimate the occurrence or magnitude of extinction debt in changing habitats, historical landscape parameters (e.g. connectivity, area) and historical human population density have often been related to current species richness (Helm et al., 2006; Piessens & Hermy, 2006; Pärtel et al., 2007). Occurrence of extinction debt is detected when current species richness is better described by historical land-use characteristics than current land-use characteristics. However, the limitation of this indirect approach is that while it provides information on whether extinction debt exists or not, it does not provide any

information whether any extinctions have already occurred or which species contribute to the existence of extinction debt. Good-quality historical datasets can provide thorough information on species dynamics occurring after habitat changes (e.g. Bahr et al., 2012; Gritsch et al., 2016; Hédl et al., 2017).

Important information on species dynamics in changing habitats can also be obtained by comparing different successional stages of the same habitat (i.e. space-for-time substitution). Rapid changes in land-use have often led to considerable variation in the current conditions of landscapes. The same landscape may consist of dynamic patches that have undergone extensive changes in environmental conditions and species composition as well as stable habitat patches that have persisted in the same condition for a long time. By comparing the species composition of habitats in different successional stages in the same landscape, we can detect the vegetation dynamics and the possible mechanisms behind the changes. This kind of knowledge is crucial for designing effective biodiversity conservation and restoration schemes (Török & Helm, 2017).

1.2. Objectives of the thesis

The main objective of this thesis was to study the dynamics of grassland plant diversity and species composition in response to habitat fragmentation, degradation and changes in environmental conditions. I applied the functional species pool approach to study what drives the community assembly in grassland ecosystems. Re-survey studies were used to detect which species suffer most under changing conditions in European grasslands and which species benefit from these changes. (**I**) In a study carried out on calcareous grassland in western Estonia, I focussed on the species assembly to detect which mechanisms drive development of community composition at different spatial scales in stable and dynamic grassland habitats. As a novelty, I applied the functional species pool approach, which allows separating biotic effects from abiotic filtering, providing more thorough insight into mechanisms governing species assembly. (**II**) In order to investigate which species are most vulnerable to habitat loss and degradation in northern Estonian calcareous grasslands, I compared species composition data from current inventories with the data from high-quality historical species survey from the same locations. The study allowed the identification of species whose populations had disappeared locally during 90 years of extensive land-use change, environmental degradation and fragmentation. The obtained knowledge allowed me to distinguish which species are most likely to contribute to the occurrence of extinction debt in semi-natural grasslands in other regions in Estonia, where habitat changes have been less severe. (**III**) To further understand how habitat change has altered community composition in northern Estonian calcareous grasslands studied in paper **II**, we also investigated which species have increased their abundance or occurrence after changed environmental conditions. We further aimed to document the changes in plant species richness and functional diversity. Moreover, we aimed to evaluate the habitat integrity of current grassland remnants compared to their

historical state prior to extensive area and habitat quality loss. (**IV**) Finally, I expanded the approach of using re-survey data for investigating species susceptibility to habitat change at the European scale. By combining the local trends of populations from different regions obtained from a wide range of re-survey studies, I investigated the general tendencies of grassland species' response to habitat change across Europe. The aim was to identify which functional trait values are associated with species susceptibility and whether intraspecific trait variability has an impact on species ability to persist in European degraded grasslands. Additionally, I estimated whether species that have been lost from European grasslands over the past century and decades carry unique trait values. Finally, based on the obtained results, I propose suggestions for grassland conservation and restoration (**I**, **II**, **III**, **IV**).

The objectives of the thesis were as follows:

1. To identify processes governing species assembly in grassland habitats with differing land-use history (**I**). More specifically I asked:
   - Are grasslands with regular and long management histories assembled differently than dynamic habitats (such as overgrowing former grasslands or novel developing grasslands) (**I**)?
   - Which processes (dispersal limitations, abiotic conditions, biotic interactions) are important in determining species assemblages at different spatial scales and with different land-use history (**I**)?

2. To study dynamics of grassland plant richness and species composition following habitat loss and decreased habitat quality. More precisely, I focused on the following questions:
   - Does the species composition differ in currently highly degraded dry calcareous grassland remnants compared to good condition historical grasslands (**II**, **III**)?
   - Have total species richness, functional diversity and integrity of grassland remnants changed over the past 90 years?
   - Which life-history traits, trait values and habitat preferences are related to species extinctions and colonisations in degraded grasslands (**II**, **III**, **IV**)?
   - Which species most likely contribute to the extinction debt in calcareous grasslands (**II**, **III**)?
   - Does the success of species in European grasslands depend on intraspecific trait variability (**IV**)?
   - Have European grasslands lost a unique part of their functional trait composition with locally decreasing species (**IV**)?
   - How has the ecosystem functional composition changed as the result of changes in species composition in European grasslands (**IV**)?

3. To develop suggestions for habitat conservation and restoration in dry calcareous grasslands and for grasslands at a larger scale (**I**, **II**, **III**, **IV**).

2. MATERIALS AND METHODS

2.1. Study locations and data collection

Studies **I**, **II** and **III** were conducted on calcareous grasslands (alvars) in two separate regions of Estonia (Fig. 1). The distribution of alvars is restricted with thin soils (generally <20 cm) on Ordovician or Silurian limestone. These highly valuable communities are characterized by a very high richness of habitat specialist plant species, especially at small scales (Paal, 1997; Pärtel et al., 1999a; Reitalu et al., 2014), but also high diversity of invertebrates and birds (Newton, 2004; Öckinger & Smith, 2006). Continuous moderate management (mainly grazing by sheep or horses and mowing) have kept them open, avoided encroachment by trees and shrubs and reduced the light competition between herbaceous species (Pärtel et al., 2007; Helm et al., 2009; Dengler et al., 2014). Abandonment of traditional management activities, destruction, intensive agriculture and eutrophication during the past century have caused a rapid decline in grassland area, increased fragmentation and succession from species-rich open grasslands to species-poor secondary forest (Kasari et al., 2013) (Fig. 2). In the 1930s the area of alvar grasslands in Estonia was estimated at more than 43 000 ha (Laasimer, 1965), while currently only 6000 ha remain, often only as fragments with atypically high and dense grass layers (Helm et al., 2006; Helm, 2011).

To test how species assembly patterns differ in grassland habitats with different land-use history (study **I**), we sampled 35 grassland complexes in two adjacent islands of Saaremaa and Muhu in western Estonia (approximately 58°N, 22°–23°E). In each of the grassland complexes, we chose one open and well-preserved calcareous grassland (hereafter 'historical grassland'), one recently overgrown grassland (hereafter 'former grassland') and one developing grassland (e.g. road verges or old fields, hereafter 'developing grassland'). The information on the status of historical grassland was obtained from historical vegetation survey maps (Laasimer 1965). Historical grasslands have been regularly managed and in a similar state for centuries (Pärtel et al., 1999b). Former grasslands were historically part of alvar grasslands, but due to the cessation of management activity and planting of pines (*Pinus sylvestris*) in the 1960s have become forest with an age of approximately 40 years. Developing grasslands were compositionally and visually similar to grasslands but have never been alvar grasslands. However, nowadays they are mostly mown annually or more frequently (in the case of road verges), open and without trees and shrubs. The variation of environmental parameters (soil depth, soil moisture, organic matter content) as well shrub and tree covers were similar among the 35 grassland complexes (**I**).

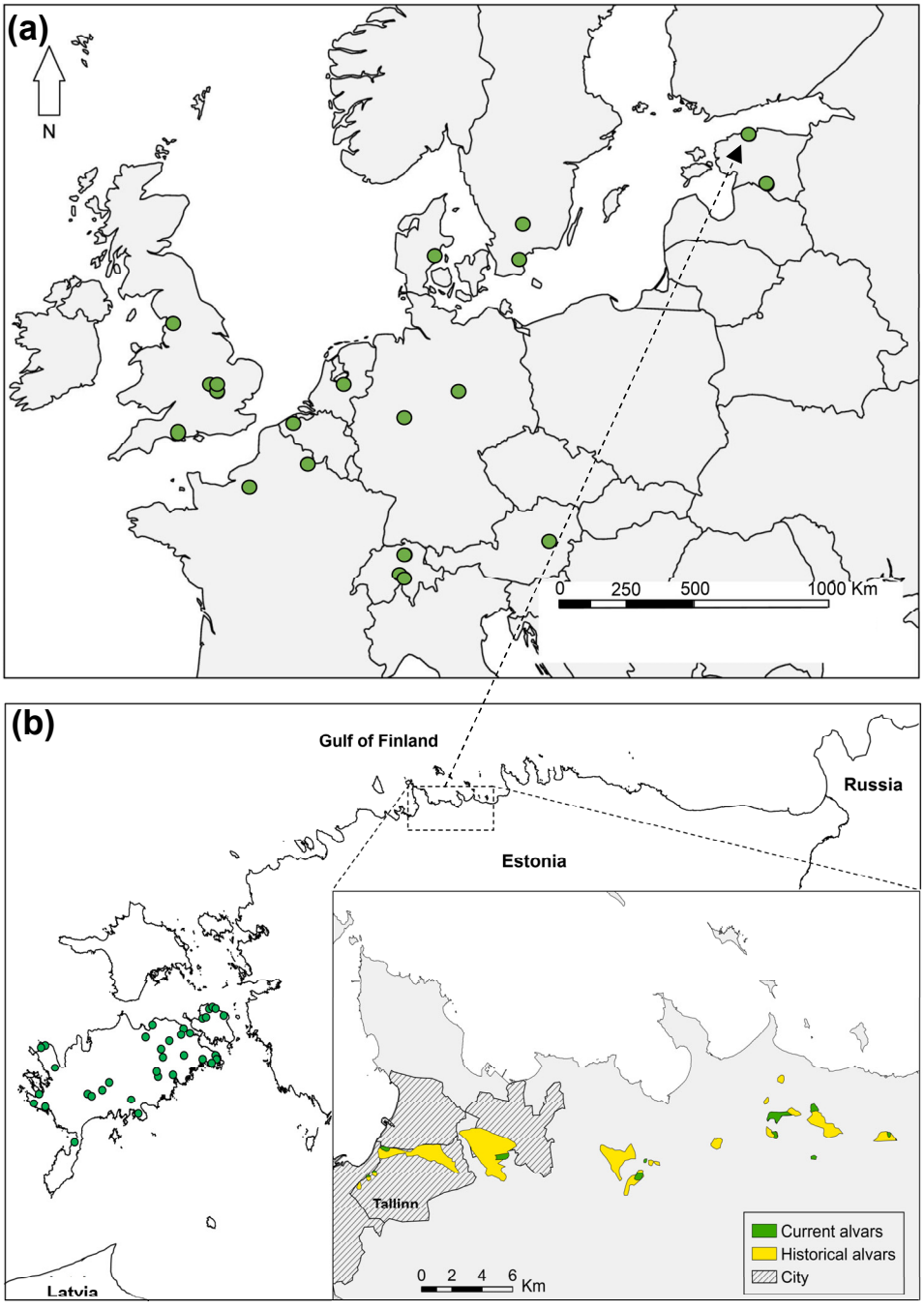

Figure 1. (a) Locations of re-survey study sites (study **IV**) in ten European countries. Green dots on the map indicate the location of each study or individual dataset by site, study region or country, depending on the information available in the source study (**IV**). (b) location of 35 study sites (green dots) in Saaremaa (larger) and Muhu (smaller) islands (**I**) and historical and current distribution of eight studied dry calcareous grasslands in northern Estonia (**II**, **III**). Modified from Fig. S1 in **I** and Fig.1 in **II**, **III**, **IV**.

In studies **II** and **III** we sampled eight alvar grasslands in northern Estonia (ca 59°N, 24°–25°E), where unique historical data was available from the years 1918–1923 (hereafter 'initial survey'). Comparison of current and historical data enabled documentation of the extinctions and colonisations of habitat characteristic plant species and changes in taxonomic and functional diversity following extensive habitat loss and degradation. The historical data were collected by Gustav Vilbaste (Vilberg, 1927), one of the leading botanist in Estonia, and includes maps (scale 1:84 000), descriptions of sampling locations and vegetation surveys of alvars prior to extensive habitat loss and degradation. Current species occurrence data was gathered from exactly the same locations during the years 2008–2012 (hereafter 'final survey').

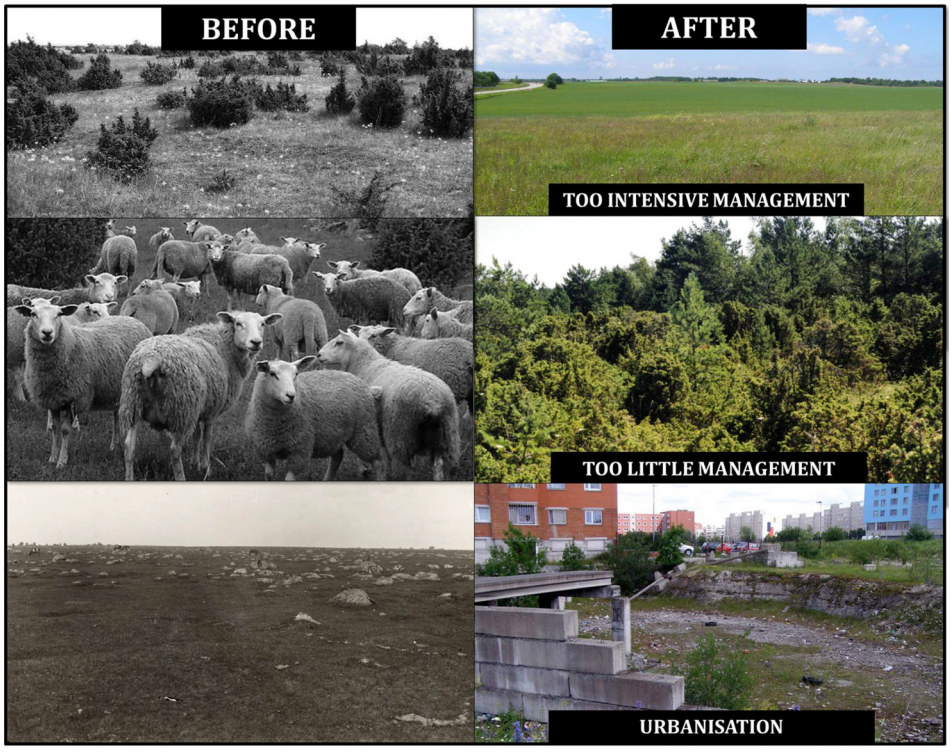

Figure 2. During the last centuries, species rich semi-natural grasslands have gone through extensive area loss and increased isolation. Additionally, remaining grassland fragments are currently with atypically high and dense grass layers. Changes are caused by too intensive agriculture, cessation of traditional management activities or urbanisation (photos by G. Vilbaste in 1922, image courtesy of Estonian National Museum Fk 1523:2523 and by A. Helm in 2008).

The current area of alvar grasslands was measured from aerial photographs supplied by the Estonian Land Board in 2008 (http://www.maaamet.ee). At least three qualified persons helped to compile detailed lists for all the vascular plant species growing in the studied sites in 2008. In 2009–2012, all the sites were

revisited to search for those populations that had been historically present, but not recorded by 2008 (**II**, **III**). Only species characteristic to alvar grasslands (i.e. 'alvar characteristic species', species that are typical to a given community and belong to its historically developed habitat-specific species pool (Helm et al., 2009; 2015) were included in the analyses (**II**).

For study **IV**, where we analysed the changes in plant composition of European grasslands over past century, we compiled information from 22 floristic re-surveys distributed across grassland fragments in 10 countries located in western, central and northern Europe (detailed information about primary study locations and data collection is available in Appendix S1 in paper **IV**). Only herbaceous vascular plant species and chamaephytes (subshrubs or dwarf shrubs) were included in the analyses; trees and shrubs were excluded (**IV**). The final dataset contained 2931 observations of site-specific population dynamic trends for 960 different taxa (species or subspecies). The plant species list was unified according to The Plant List (http://www.theplantlist.org/) using the function TPL in package Taxonstand (Cayuela et al., 2012) in R (R Development Core Team 2017).

2.2. Assembly patterns in grassland habitats with different land-use history

We used the functional species pool framework suggested by de Bello et al. (2012) to distinguish biotic and dispersal-related effects from environmental filtering (**I**). This approach enables estimation of the assembly patterns by testing the trait divergence or convergence at finer scales in comparison with the patterns at broader scales. Selected scales included (1) 'plot scale', consisting of species abundance data of all vascular plant species from the 2 × 2 m sample plots, (2) 'local community' scale, consisting of species occurrence data in the area of an approximately 50-m radius surrounding the 2 × 2 m plots, and (3) 'habitat-specific species pool' at the broadest scale, compiled as cumulative list of species sampled from 35 sites of respective grassland (see Figure S2, in Supporting Information of paper **I**). These scales represent small-scale interactions at the plot level and species accumulation at the community level.

2.3. Changes in species richness, composition and functional diversity following habitat conversion

To observe changes in taxonomic diversity in historical and current communities, we calculated species richness (i.e. the total number of vascular plant species in each grassland site) (**III**).

In order to study which species are most prone to local extinctions and which ones can colonise and survive in currently highly modified grassland patches, species occurrence data from the initial and in final surveys were compared (**II**, **III**). For estimating species populations' probability for local extinctions, we calculated the species extinction coefficient for every specialist species by using the following formula (**II**):

$$\text{Species extinction coefficient} = \frac{(\text{number of populations gone extinct by 2011})^2}{\text{number of populations present in 1923}}$$

The formula gives greater value for species lost from more populations in eight alvar grassland remnants. Therefore, a random disappearance from one population or an unrecorded species in a single population has relatively little effect on the calculated extinction coefficient.

In paper **III** and **IV** we provided one of five possible trend estimates (hereafter 'species local trend') for every species in each dataset individually. According to changes in species occurrences or abundances between the initial and final survey, species were considered either: (1) extinct species – species that were listed in historical datasets, but were absent in the final survey; (2) declining species – species whose occurrence had decreased between the initial and final survey (**IV**) or species whose occurrence has decreased by at least two sites (**III**); (3) stable species – species whose occurrence had remained stable between the initial and the final survey or showed relatively small change; (4) increasing species – species whose occurrence had increased (**IV**) or whose occurrence increased by at least two sites (**III**); and (5) new species – species that were not listed in the initial survey, but were recorded in the final survey (**III**, **IV**). Identifying the locally 'extinct' and 'new' species was rather straightforward, whereas to determine whether a species had a 'stable', 'increasing' or 'decreasing' trend, different approaches depending on the available information were used (see details from Methods and Table 1 in paper **IV**). In paper **IV**, we used three trend groups instead the original five for statistical analyses – 'losers' (consisting of extinct and declining species), stable species (no trend in time) and 'winners' (consisting of increasing and new species) in further analyses (**IV**).

2.4. Habitat integrity

The changes in species composition over the past 90 years were tested with ordination biplot by redundancy analysis (RDA), using current and historical species occurrence data at eight studied alvars, and species' mean preference for nutrient availability (Ellenberg N) and light requirement (Ellenberg L) values (**III**). In order to analyse the change in habitat integrity and conservation value, we used the Index of Favourable Conservation Status (FCSi), suggested by Helm et al. (2015). FCSi is a log-ratio of characteristic (i.e. the number of species that are typical to a given community and belong to its historically developed habitat-specific species pool) and derived diversity (i.e. species that have not been historically characteristic to a given habitat but have newly occupied the sites). Consequently, habitat integrity is higher with relatively higher characteristic and smaller derived diversity. Regional community surveys and expert opinions were used to differentiate species that are characteristic to a given habitat type and belong to its historically developed species pool. All other species recorded in the sites were included in derived diversity.

2.5. Life-history traits and habitat preferences of losers and winners

A number of life-history traits and Ellenberg indicator values (Ellenberg et al., 1991) were used to study which filters act for local assemblages with different land-use history at finer and broader spatial scales (**I**) and to identify whether and which species characteristics and habitat requirements are related to local extinction or colonization of plant populations in grasslands during the last 90 years (**II**, **III**) and up to the past 300 years (**IV**). The selected traits reflect species growth and competitiveness (average plant height (m), specific leaf area (SLA, $cm^2\ g^{-1}$), strategy type), dispersal and establishment abilities (mean seed weight (mg), dispersal distance (m), dispersal mechanism, number of seeds per shoot, terminal velocity of diaspores (m/s), total seed mass per shoot (average seed weight multiplied by number of seeds per shoot)), persistence and reproduction abilities (length of flowering period, life span, main pollen vector, mode of reproduction, compatibility, seedbank longevity), species tolerance of anthropogenic influences (urbanity) and mycorrhizal association (mycorrhizal status) (see categories of categorical traits from Methods in papers **I**, **II**, **III**, **IV** for the complete list). To estimate the effect of intraspecific trait variability on species local trend in paper **IV**, intraspecific trait variability, expressed by the coefficient of variation (CV), was calculated for the four continuous traits (seed weight, plant height, specific leaf area, and terminal velocity), by using data from the TRY database (Kattge et al., 2011) (**IV**). We also studied whether species habitat requirements determined their trends, by using Ellenberg indicator values for light (L) and soil nitrogen content (N) (**II**, **III**, **IV**), soil

moisture (F), continentality (K), soil reaction (R), and temperature (T) (**IV**) (Ellenberg et al., 1991).

Species functional traits and habitat requirement values were obtained from databases and additional information was extracted from the literature (see Methods in papers **I**, **II**, **III**, **IV** for a complete list). All life-history traits used in the analyses were tested for normality and log-transformed when necessary.

2.6. Statistical analyses

Trait convergence and divergence patterns as well the changes in functional diversity were tested by using mean pairwise trait dissimilarity (MPD), which estimates the dissimilarity between all pairs of species in terms of their mean trait values (**I**, **III**). We computed functional diversity values for each trait individually and for all traits together (**I**, **III**) to observe differences across multiple niche axes (de Bello et al., 2013). In study **I** we then calculated the effect size (ES), i.e. the difference in MPD between scales, for: (1) finer scale: MPD at the plot scale minus MPD at the local community scale ($ES_{fine} = MPD_{plot} - MPD_{community}$), (2) broader scale: MPD at the local community scale minus MPD at the habitat-specific species pool scale ($ES_{broad} = MPD_{community} - MPD_{habitat}$). ES indicates here the strength and direction of different assembly processes (de Bello et al., 2012) operating behind the divergence or convergence patterns at different scales. For example, negative ES_{fine} at the finer scale would indicate convergence, probably driven by weaker competitor exclusion or non-suitable phenotypes exclusion, while positive ES_{fine} indicates divergence, likely driven by limiting similarity (Adler et al., 2010; de Bello et al., 2012), although other biotic effects operating on convergence and divergence are not totally eliminated.

In order to study which trait values filter species from the local community species pool to the plot level (**I**), we computed community weighted means (hereafter CWM) for 2 × 2 m sample plots and compared them to the mean trait value of the species at the broader scale but that do not occur in the 2 × 2 m plots, following Riibak et al. (2015). CWM was also calculated to estimate the effect of functional traits and environmental requirements in determining species susceptibility to habitat change in northern Estonian alvars (**III**). Trait dissimilarity between species and CWM values were calculated with the *FD* package (version 1.0-12; (Laliberté & Legendre, 2010; Laliberté et al., 2014) in R (R Development Core Team 2016) and mean trait dissimilarity with the *picante* package (version 1.3-0, Kembel et al., 2010) (**I**, **III**). Linear regression was used to test whether the change in habitat area (i.e. historical–current values) has influenced the change in different diversity measures (**III**).

Considering phylogenetic similarities among species belonging to the same phylogenetic group (**II**) and to eliminate possible phylogenetic pseudoreplication (Tremlová & Münzbergová, 2007; Bielby et al., 2010), the strength of phylogenetic signal of selected life-history traits and habitat preferences was

tested with the *picante* package (Kembel et al., 2010) in R (Table S3 in Supporting Information study **II**). Less abundant species with unresolved phylogeny in the initial study were excluded from further analysis. The phylogenetic tree was made ultrametric. The effects of life-history traits and habitat preferences on species extinction coefficient were analysed with generalized estimating equations (GEE) analyses, generated by the phylogenetic comparative methods *ape* package (Paradis & Claude, 2002; Paradis et al., 2004) (**II**).

To test the effect of functional traits and habitat requirements on species local trend (ordinal response variable with three levels – losers-stable-winners), we fitted cumulative link mixed models (CLMMs) with a logit link function in the 'ordinal' package (version 2015.6-28; Christensen, 2016) in R (**IV**). In addition to a fixed predictor (species functional trait/habitat requirement) I included in each model 'study' and 'species' as two random effects to account for the non-randomness of observations. Additional post-hoc tests were conducted with the 'lsmeans' package for categorical fixed factors (Lenth, 2016). Species richness, habitat area, functional traits and environmental requirements were tested for normality, log-transformed or square root transformed when necessary. Paired *t* tests were used to estimate the difference of the effect size from zero (**I**), to compare taxonomic and functional diversity (**III**), community mean functional traits (**I**, **III**) and FCSi values of current and historical communities (**III**). Statistical analyses were considered significant at $P < 0.05$.

For the nine European datasets with the most complete species survey data (i.e. where the full information on the species composition was provided; the studies included in this analysis can be seen in Appendix S1, **IV**), we calculated the functional distinctiveness (uniqueness; Violle et al., 2017) of 'losers', stable species and 'winners'. In each study, the functional distinctiveness of each species was calculated as the dissimilarity of the traits of each species with respect to the centre of the pool of species in that particular study. For this, we used the 'funrar' R package (Grenié et al., 2017), considered all the available traits, and estimating species dissimilarities by means of the Gower distance. The difference between distinctiveness of loser, stable and winner species were tested by means of a mixed effects model in the 'lme4' R package (Bates et al., 2015), where the trend group was used as a fixed factor and the study as a random factor, followed by a Tukey test to detect significant differences between pairs of groups.

3. RESULTS

3.1. Assembly patterns in historical, former and developing grasslands

Our results revealed that grasslands with regular and long management histories are assembled differently compared to dynamic habitats (**I**). In historical grasslands, divergence patterns prevailed at the finer scale (i.e. species filtered from local community to plot) when eight traits were pooled ($ES_{fine} > 0$, Fig. 3a). Results of individual traits indicated that divergence in finer-scale assembly in historical grasslands was determined mostly by divergence patterns for pollen vector and for mode of reproduction ($ES_{fine} > 0$, Fig. 4c, f), while a number of traits showed random patterns (dispersal mechanism, life span, plant height, SLA, Fig. 4a, b, d, g; see Electronic Supplementary Material (ESM) Table S3 in **I**) and convergence patterns prevailed for mean seed weight and terminal velocity ($ES_{fine} < 0$, Fig. 4e, h). Analyses based on community weighted mean traits indicated that species assembled to plots were shorter, had on average lower mean seed weight, lower SLA, lower terminal velocity, were more often clonal and less pollinated by insects than species not present in plots (see Table 1 in **I**).

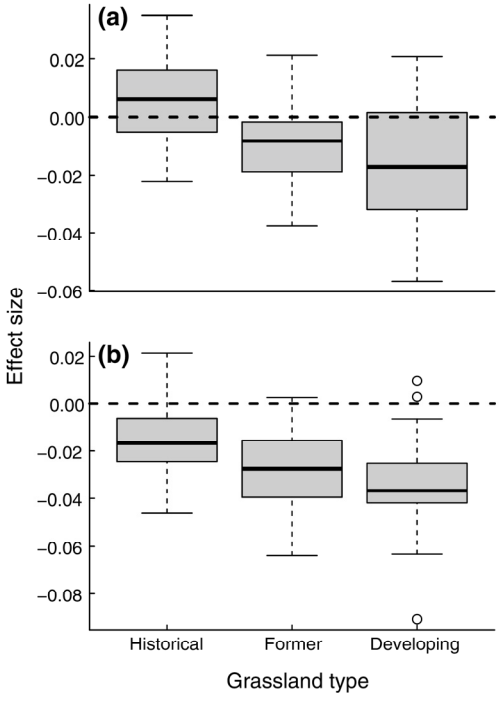

Figure 3. The mean trait dissimilarity (indicated by effect size) between species a) filtered from the local community into 2 × 2 m plots and b) from the habitat species pool to local communities in grasslands with different development histories across all analysed traits (**I**). The dotted line indicates that the effect size is zero, results above zero indicate 'divergence', below zero 'convergence'. In all cases the grey boxplots indicate that the effect size significantly differs from zero ($P < 0.05$). In box plots, the median for each data set is indicated by the heavy central line, and the first and third quartiles are the lower and upper edges of each box. Individual points indicate outliers. Figure reproduced from paper **I**

In dynamic habitats, i.e. in both former and developing grasslands, significant trait convergence was detected at the finer scale when eight traits were pooled ($ES_{fine} < 0$, Fig. 3a, see ESM Table S3 in **I**). Individual trait analyses indicated that finer-scale assembly was governed mostly by convergence patterns (for dispersal mechanism, life span and terminal velocity in both type of dynamic grasslands, as well for mean seed weight and SLA in former grasslands and for mode of reproduction in developing grasslands ($ES_{fine} < 0$, Fig. 4a, b, e, g, h). Significant divergence was detected for main pollen vector and plant height ($ES_{fine} > 0$, Fig. 4c, d) and random pattern for reproduction mechanism (Fig. 4f) in former grasslands and for pollen vector, plant height, seed weight and SLA in developing grasslands (Fig. 4c, d, e, g). Comparison of mean trait values indicated that species in plots of former grasslands were shorter, had lower SLA, were more often perennials and without wind-dispersal capacity compared to species not present in plots (see Table 1 in **I**). At the same time, results from developing grasslands revealed that species with higher terminal velocity, lower height, longer life span, dispersal by other means than wind and pollination without insects were prevailing at the plot scale compared to those not recorded in plots (see Table 1, **I**).

At broader scales, i.e. species filtered from the habitat species pool to the local community, significant convergence patterns were detected for both historical and dynamical grasslands ($ES_{broad} < 0$, Fig. 3b, ESM Table S3 in **I**). Convergence patterns also dominated for individual traits; species with more similar life span, seed weight, mode of reproduction, SLA and terminal velocity were filtered from habitat species pool to local community ($ES_{broad} < 0$, Fig. 5b, e–h) in historical and former grasslands. Significant divergence occurred only for mean plant height at broader scale of historical and former grasslands ($ES_{broad} > 0$, Fig. 5d). Dispersal mechanism and main pollen vector exhibited random patterns in historical grasslands (Fig. 5a, c), while a divergence pattern was detected for pollen vector in developing grasslands ($ES_{broad} > 0$, Fig. 5c).

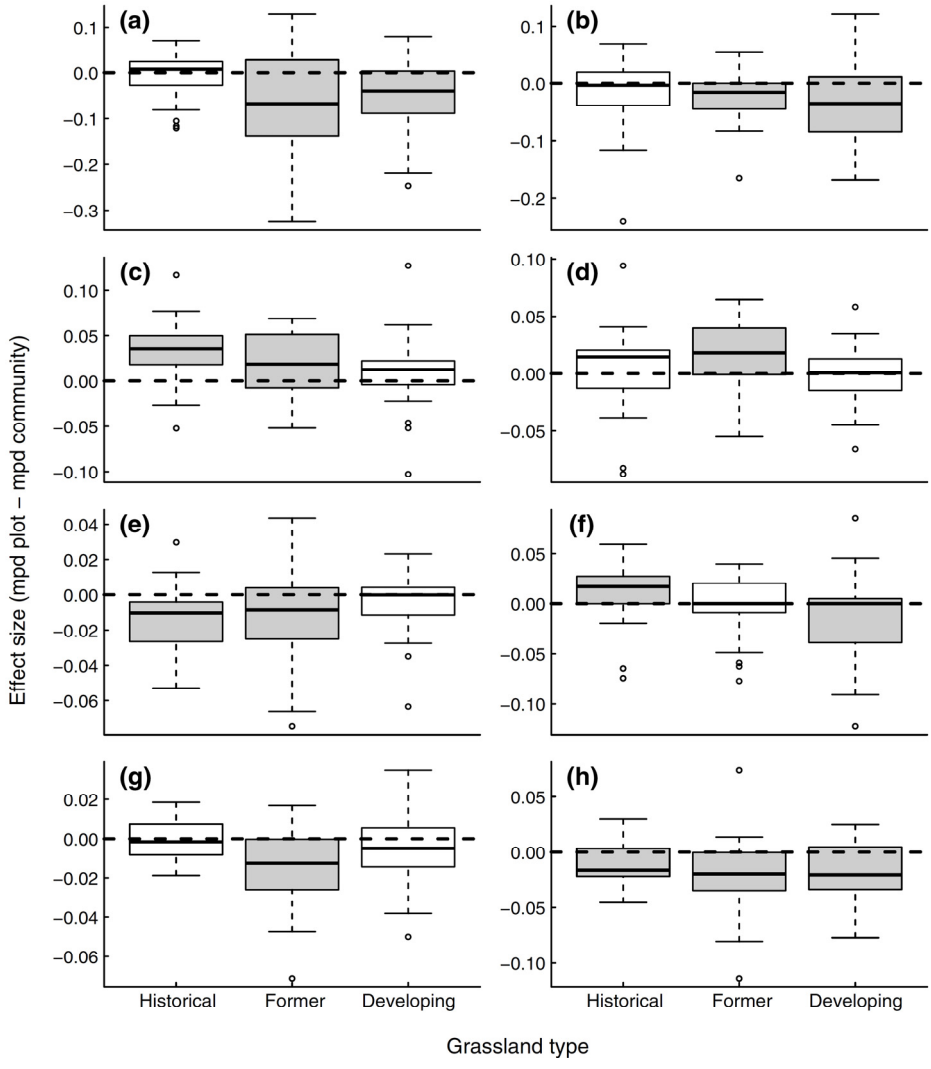

Figure 4. The mean trait dissimilarity (indicated by effect size) between species filtered from the local community into 2×2 m plots in grasslands with different development histories for individual traits: a) dispersal mechanism, b) life span, c) main pollen vector, d) mean plant height, e) mean seed weight, f) mode of reproduction, g) specific leaf area, and h) terminal velocity (**I**). The dotted line indicates that the effect size is zero, results above zero indicate 'divergence', below zero 'convergence'. Filled boxplots indicate that the effect size significantly differs from zero ($P < 0.05$). See Fig. 3 legend for description of box plots. Figure reproduced from paper **I**

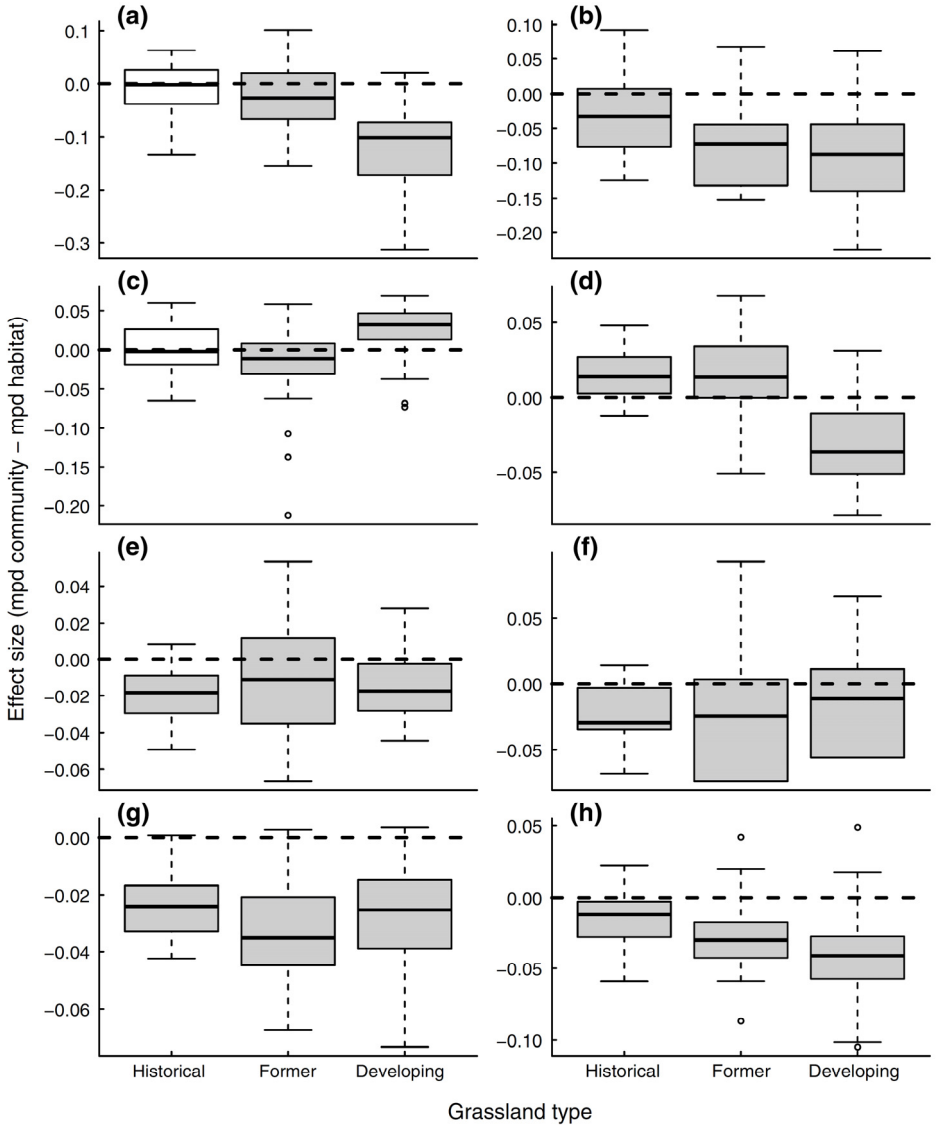

Figure 5. The mean trait dissimilarity (indicated by effect size) between species filtered from the habitat species pool into local communities in grasslands with different development histories for individual traits: a) dispersal mechanism, b) life span, c) main pollen vector, d) mean plant height, e) mean seed weight, f) mode of reproduction, g) specific leaf area, and h) terminal velocity (**I**). The dotted line indicates that the effect size is zero, results above zero indicate divergence, below zero convergence. Filled boxplots indicate that the effect size significantly differs from zero ($P < 0.05$). See Fig. 3 legend for description of box plots. Figure reproduced from paper **I**

3.2. Changes in taxonomic and functional diversity and habitat integrity of calcareous grasslands in northern Estonia

Historically, the sizes of the eight studied habitat patches ranged from 0.16 to 6.36 km^2, while currently only small and isolated remnants, ranging from 0.002 to 0.7 km^2, have remained (**II**, **III**). Thus, during the last 90 years the studied alvar grasslands have lost approximately 90% of their total area and nearly one third of the original specialist species with an average loss of 21 specialist species per site (**II**). Compared to the years 1918–1923, in total 71 species (168 populations) had disappeared locally (Table S1 in Supporting Information of paper **II).** However, the total number of species over all eight study sites is currently greater than historically, as is species richness per site ($t = 3.99$, $df = 7$, $P = 0.005$) and functional diversity when 11 functional traits were pooled (**III**). Functional diversity of four traits (seed weight, dispersal type, SLA, terminal velocity) had increased in current communities, while functional diversity of plant height had decreased (Table 1, in **III**). CWM of seed weight, terminal velocity and plant height had increased, whereas CWM of dispersal type and SLA remained the same (Online resource 5 in **III**). Extinction coefficients were also higher for short-lived and non-clonal species with lower average height, higher preference for light and lower preference for soil nitrogen content (**III**). Habitat area was not related to the changes in species richness and functional diversity ($t = –0.524$, $P = 0.628$; $t = –0.415$, $P = 0.699$, accordingly).

Current and historical sites grouped distinctly in RDA ordination, indicating changes in species composition during the past 90 years (Online Resource 6) (**III**). The Index of Favourable Conservation Status (FCSi) (i.e. log-ratio of characteristic to derived diversity) is currently significantly smaller than in the initial survey ($t = –4.098$, $df = 7$, $P = 0.004$). Despite the increased total species richness, the habitat integrity and conservation value of the studied sites are currently significantly lower compared to the historical survey. On average 35 derived species (i.e. newly colonized native species from other habitat types) per site were recorded historically, while the same parameter is currently 75. However, the mean number of characteristic species had not changed significantly over time (about 60 characteristic species per site were recorded in both historical and current communities (Online Resource 2 in **III**).

3.3. Losers and winners during grassland degradation

Species more sensitive to land-use change in Estonian degraded dry calcareous grasslands (‘losers’) had lighter and fewer seeds, lower seed terminal velocity, and were more likely self-pollinated and dispersed by wind (**II**, **III**) (Table 1). Losers were also characterized by lower average height, shorter life span (**II**, but see **III**), lack of clonal growth and higher sensitivity to changes in the biotic

and abiotic conditions of the sites (indicated by lower soil nitrogen requirement and higher preferences for light) compared to more persistent species (**II**, **III**). Local extinctions of populations were not correlated with seed bank longevity or flowering duration (**II**). However, when phylogenetic affinity of studied species was not taken into account, winners had longer flowering period (**III**).

Table 1. Generalized estimating equations (GEE) analyses of the effects of life-history trait values and habitat preferences on species extinction coefficient in alvar grasslands of northern Estonia. A negative trait effect indicates a negative relationship between traits or habitat preferences and the extinction coefficient. Statistically significant relationships are marked in bold. The degrees of phylogenetic freedom (d.f.P) were calculated as a part of the analysis. Table is modified from paper **II**.

Trait	Trait effect (±SE)	No of obs.	P	t	F	d.f.	d.f.P
Dispersal mechanism		**98**	**		**6.47**	**2**	
'wind'	**0.68 (±0.270)**		*	**2.52**			**26.79**
'other'	0.36 (±0.208)			1.76			26.79
Flower duration	–0.10 (±0.056)	118		–1.79			29.27
Life span		**121**	*		**4.31**	**1**	
'annual, biennial'	**0.33 (±0.159)**		*	2.08			**29.60**
Mode of reproduction		**121**	*		**4.99**	**2**	
'only by seeds or spores'	**0.28 (±0.127)**		*	**2.18**			**29.60**
'mostly by seed, rarely vegetatively'	0.21 (±0.198)			1.05			29.60
Pollen vector		**112**	**		**7.76**	**2**	
'wind'	0.02 (±0.227)			0.09			29.90
'self-pollination'	**0.39 (±0.149)**		*	**2.60**			**29.90**
Plant height	**–0.02 (±0.003)**	**97**	***	**–5.51**			**27.00**
Seed bank longevity		93			2.02	2	
'transient < 1year'	–0.14 (±0.206)			–0.67			26.11
'persistent >1 years'	0.14 (±0.172)			0.82			26.11
Seed number (log)	**–0.58 (±0.076)**	**95**	***	**–7.49**			**27.36**
Seed weight (log)	**–0.17 (±0.055)**	**117**	**	**–3.04**			**29.09**
Terminal velocity (log)	**–0.75 (±0.187)**	**69**	***	**–4.01**			**23.11**
Total seed mass per shoot (log)	**–0.24 (±0.028)**	**93**	***	**–8.43**			**27.00**
Ellenberg L	**0.18 (±0.055)**	**118**	**	**3.23**			**29.33**
Ellenberg N	**–0.39 (±0.111)**	**109**	**	**–3.54**			**28.33**

No of obs. – the number of species included in the analysis, *t* – *t*-value of the coefficient estimate. Significance levels – *** P < 0.001, ** P = 0.001–0.01, * P = 0.01–0.05

In analysing data from 22 European grassland re-surveys (**IV**), species local trend was significantly determined by species competitive ability, dispersal ability and mycorrhizal status (Fig. 6–8). Species more prone to local extinctions were characterized by lower average height, lower SLA, ruderal, stress or mixed strategy, lighter seeds, lower terminal velocity, and they more likely dispersed via anemochory or by a range of other dispersal means (a mixed group including myrmecochory, man, ballistic or autochory). Losers were more likely non-mycorrhizal or obligately mycorrhizal, while more successful species populations were more likely to be facultatively mycorrhizal (Fig. 6–8). Among the traits related to persistence and reproduction, the mode of reproduction and seedbank longevity had a significant effect on species local trend, indicating that winners had more probably vegetative propagation ability and persistent seed bank. Species tolerance of anthropogenic influences (urbanity) also had a significant effect; more successful species were more likely urbanoneutral, while species prone to local extinctions were more likely urbanophobic species (Fig. 6–7). Species local trend was not determined by life span, compatibility, maximum dispersal distance and by the intraspecific trait variability of the tested continuous traits. Although pollen vector was deemed significant according to the CLMM, the post-hoc analyses did not find any significant differences between the different pollen vectors. Species more prone to local extinctions were characterized by a preference for lower soil nitrogen content, lower soil reaction and lower temperature, but for higher light conditions ($P < 0.05$; Fig. 6). Species preferences for continentality and humidity had no significant effect on species local trend ($P > 0.05$).

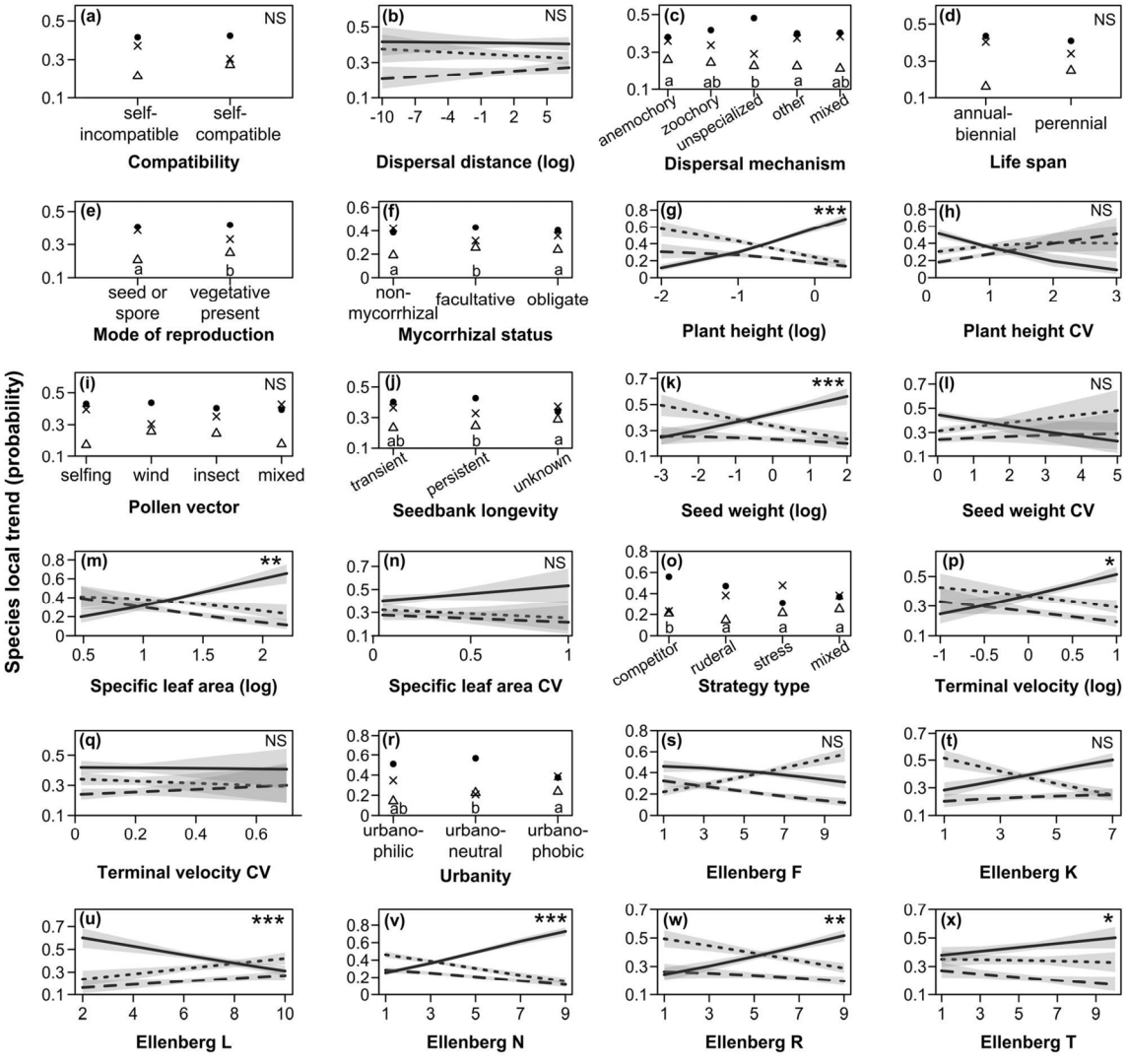

Figure 6. Results of cumulative link mixed model (CLMM) analyses of the effects of life-history trait or intraspecific trait variability values and habitat preference related to species local trend with three ordinal categories: losers (dotted line and crosses), stable (dashed line and triangles), winners (continuous line and dots). Statistically significant tests for CLMM analyses (continuous traits) and Tukey post-hoc tests (categorical traits) are marked by asterisks (*** $P < 0.001$, ** $P = 0.001–0.01$, * $P = 0.01–0.05$), non-significant ones by 'NS' ($P > 0.05$). The labels denote homogeneity groups based on Tukey post-hoc comparisons (**IV**). Figure modified from paper **IV**

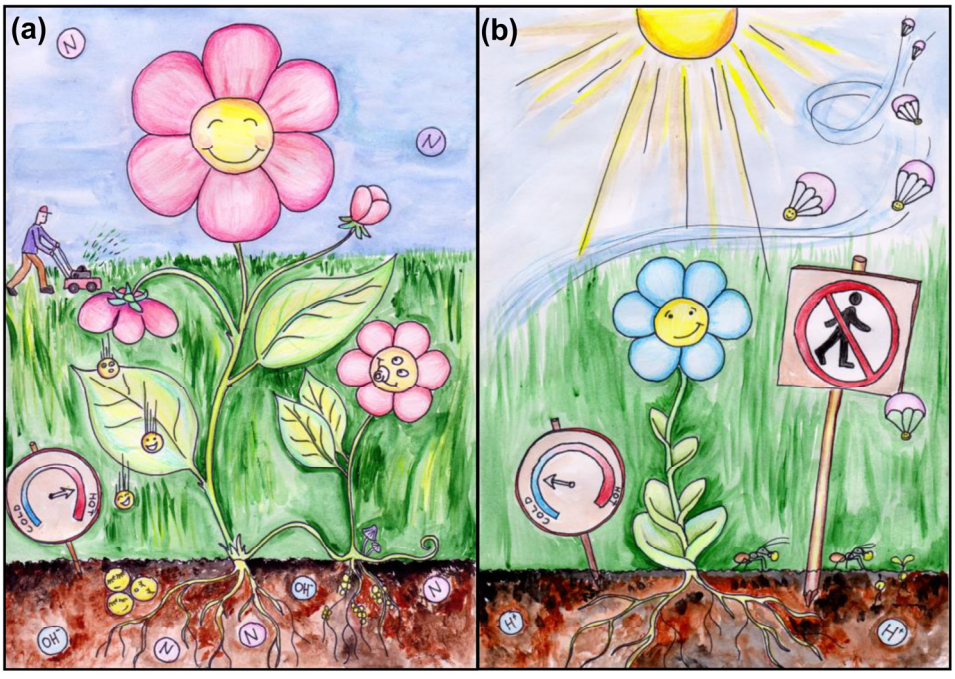

Figure 7. Comparisons of winners (a) and losers (b) in European grasslands. More successful were species characterized by higher average height, greater SLA, heavier seeds and higher seed terminal velocity. Losers had more likely short-lived seedbank, anemochory or other (a mixed group including myrmecochory, man, ballistic or autochory) as a dispersal mechanism, whereas winners had more likely unspecialised dispersal. Losers are also urbanophobic and they have different environmental preferences (lower soil reaction, temperature and nitrogen content preferences, but higher preferences for light availability) compared to winners (**IV**)

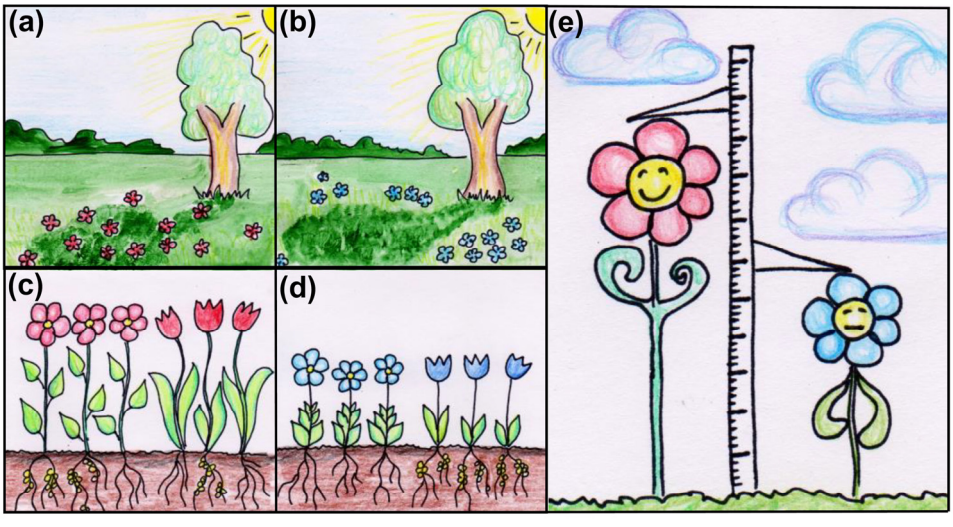

Figure 8. Compared to losers (b), winners in European grasslands with extensive land-use changes are species with higher shade tolerance (a) and with facultative mychorrhiza (c), while more prone to local extinctions are nonmycorrhizal or obligately mycorrhizal species (d) and shorter species (e) (**IV**)

3.4. Distinctiveness of species with different local trends

Functional distinctiveness analyses revealed that species more prone to local extinctions tended to have more unique traits with respect to the pool of species in each dataset than stable species, whereas increasing and new species had intermediate uniqueness result (Fig. 9).

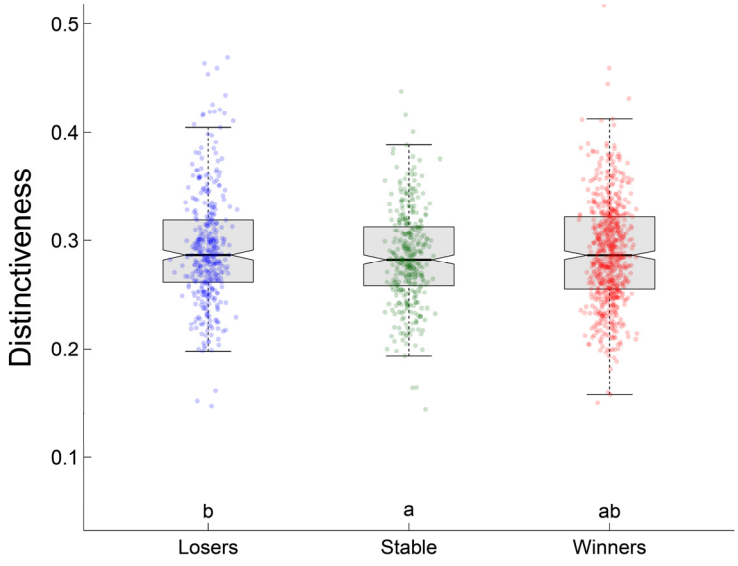

Figure 9. Functional distinctiveness of species classified according to their local trend (**IV**). For each species and study considered, we estimated its functional distinctiveness with respect to the pool of species considered in that study. Species with higher distinctiveness are more functionally different from the rest of species in the study than species with lower distinctiveness (i.e. they are more functionally unique). Different letters between groups indicate significant difference in means according to a Tukey post-hoc test. Figure modified from paper **IV**

4. DISCUSSION

Ongoing habitat destruction and fragmentation are the major threats to biodiversity, often resulting in changes in species composition. This thesis focused on the dynamics of grassland plant diversity and species composition in response to land-use change, extensive fragmentation and environmental degradation. Firstly, by studying grasslands with different land-use history in western Estonia, I found that stable grasslands with long and regular management were assembled differently than abandoned and novel developing grasslands, but these differences become evident only at finer scales (**I**). Secondly, by comparing current vegetation data with high-quality historical datasets from calcareous grasslands in northern Estonia, I found that populations more susceptible to local extinctions after changes in land-use and environmental conditions were characterized by certain life-history traits and habitat preferences (**II**, **III**). Analysing re-survey data from 22 studies conducted in European grasslands, I examined the general trends of grassland species response to habitat change over the past century or decades and found that a unique part of trait values is disappearing with decreasing species compared to more persistent species, indicating possible changes in ecosystem functions and services (**IV**).

4.1. Trait and assembly patterns depending on land-use history of grasslands and the scale of observation

Grassland management and habitat history affected strongly species co-occurrence patterns in observed grasslands complexes (**I**). In line with our hypothesis, at small scales, species with dissimilar traits occurred together in grasslands with long management history, whereas species with more similar traits occurred together in more dynamic grasslands. This result indicates that different mechanisms are operating for species assembly depending on the stability of management activity or disturbance regime of habitats. Niche differentiation governs species assembly at finer scales in historical grasslands likely due to limiting similarity (MacArthur & Levins, 1967; Stubbs & Wilson, 2004; Adler et al., 2010), while convergence patterns prevail in abandoned and developing grasslands, likely as the result of exclusion of species with non-suitable phenotypes (Schleuning et al., 2009; Batalha et al., 2015, but see de Bello et al., 2013).

Studies conducted in grazed grasslands suggest that moderate continuous management can most likely be the driver of trait differentiation at finer scales (de Bello et al., 2013; Laliberté et al., 2013). Grazing suppresses above-ground competition and allows co-existence of functionally dissimilar species (Grime, 2006; de Bello et al., 2013). Cessation of grazing results in accumulation of litter and encroachment by trees and shrubs, favouring dominance of tall, shade-tolerant species and causing local extinctions of small, light-demanding plant species with adaptations to tolerate and benefit from moderate disturbances

(Vandewalle et al., 2014; Neuenkamp et al., 2016), **II**, **III**). Yet habitats with short history of management or natural grazing have shown divergence at finer scales (e.g. Stubbs & Wilson, 2004; Bennett et al., 2013), suggesting also the importance of stability and long history of species assembly and not the effect of management per se.

Individual trait analyses highlighted that co-occurring species at the plot level in historical grasslands were functionally more dissimilar in their reproduction traits (pollination mode and in ability to reproduce vegetatively) and more similar in their dispersal traits (i.e. smaller seeds and lower terminal velocity, indicating their better dispersal ability (Westoby, 1998) than expected from the composition of the community pool (Fig. 4) (**I**). Both differences in regeneration traits, as well as better dispersal ability, are suggested to contribute to the long-term persistence of populations and high species richness in calcareous grasslands (Eriksson, 1996; Thompson et al., 1996; Maurer et al., 2003). In addition, comparison of current and historical data in dry calcareous grasslands of northern Estonia revealed that species more prone to local extinctions were characterized by specific tendencies in reproduction and persistence related traits (self-pollination, shorter life span, and lack of clonal growth) (**II**). Also, functional diversity of dispersal mechanisms (i.e. dispersal by animal, disperal by other means) was smaller according to historical species data from grasslands, demonstrating that species with certain dispersal traits were historically favoured (**III**). Dissimilarity in pollination mode and clonality in long-managed grasslands can be caused by niche differentiation due to limiting similarity (MacArthur & Levins, 1967; Stubbs & Wilson, 2004; Adler et al., 2010), but also due to regular moderate disturbance that suppresses competitive dominance at finer scales and/or facilitates the co-existence of species with different strategies (Grime, 2006; de Bello et al., 2013; Laliberté et al., 2013; Vandewalle et al., 2014). Species with more similar dispersal traits can co-occur at finer scales due to more efficient re-colonisation abilities of suitable (micro)sites (Riibak et al., 2015). Also, grazing is suggested to favour plants with smaller seeds (Eriksson & Eriksson, 1997). Competitive exclusion, as the main mechanism behind convergence patterns, is less probable to occur in historical grasslands, as small-seeded species are usually also considered to be weaker competitors for light and establishment space (Westoby, 1998).

Convergence in dispersal-related traits at the finer scale in former grasslands indicates that dispersal ability acts as an important filter during formation of species assembly in succession from open grassland to forested grassland (**I**). Species with more similar dispersal traits grow together likely due to exclusion of non-suitable phenotypes (Chesson, 2000; Grime, 2006; de Bello et al., 2012). As found in studies **II**, **III**, **IV**, and also confirmed by other studies carried out in remnant grasslands (Tremlova & Münzbergova, 2007; Neuenkamp et al., 2016), species with better dispersal capacity are not favoured in fragmented landscapes. Convergence patterns in former grasslands for life span, specific leaf area, dispersal mechanism, seed weight and terminal velocity, coupled with significantly decreased prevalence of species with short life-span and wind

dispersal as well lower SLA, can be related directly to the cessation of grazing, overgrowing by shrubs and trees, disappearance of light-demanding grassland species and colonisation of shade-tolerant forest species. Contrary to expectations, significant divergence in plant height – a trait which is positively related to dispersal ability, growth rate, nutrient availability and above-ground competitive ability (Weiher et al., 1999; Grime, 2006) – was detected in former grasslands at finer scales, indicating the importance of niche differentiation in former grasslands. This result contradicts previous expectations that traits linked to competitive ability show convergence (Grime, 2006), but also the results of papers **II**, **III**, **IV**, where species height was an important trait affecting species sensitivity to local extinctions in currently degraded grasslands. Due to trade-offs between plant height and tolerance of environmental stress, abandonment of grazing or mowing has often caused an increase in vegetation height (Cornelissen et al., 2003). However, divergence in plant height in former grasslands may also be triggered by extinction debt (Helm et al., 2006; Gazol et al., 2012). As former grasslands were previously open grasslands, the divergence in plant height and pollination mode, as well as the random pattern in mode of reproduction at finer scales can be legacies from the previous land-use type. Moreover, historical grasslands in studies **I** and **III** belong to the same grassland type with similar environmental conditions. Yet the different results of functional traits of species in western and northern Estonia alvars suggest that extinction debt is possibly already paid in the observed northern Estonia alvar grasslands, while it can still be detected in grasslands in the western part of Estonia. In developing grasslands, co-existing species at both plot scale and community level were selected by traits linked with reproduction, persistence or dispersal, which showed convergence patterns. Also, as found previously in a road verge plant community, successful colonisers were characterised by more similar life-history traits (Thompson et al., 2010). Co-existence of species with more similar dispersal traits (dispersal mechanism, terminal velocity), as well as with more similar persistence traits (e.g. life span and mode of reproduction) indicates that competitive exclusion can be the central mechanism in determining species assembly in novel grasslands. Assembly in novel grasslands is rather related to species' ability to persist through succession and compete with neighbouring individuals than to colonization ability. This can be concluded when considering the trade-off between dispersal ability and persistence ability (Westoby, 1998), as well as the results that species with poor dispersal ability (i.e. species without wind dispersal capacity, with higher terminal velocity, lower height), but with better persistence ability (i.e. perennials) were over-represented at the plot level.

Irrespective of land-use history, convergence patterns became more prevalent in all grassland types with increasing scale, indicating that different mechanisms govern species assembly at different spatial scales and developmental stages (**I**). Our results are consistent with previous findings suggesting the prevalence of convergence patterns at broader spatial scales (Götzenberger et al., 2012; de Bello et al., 2013). Biotic interactions, which act upon individual

plants, are more likely to be detected at finer scales, whereas at broader scales, interactions among all of the individual plants are unlikely, allowing trait convergence due to environmental filtering and dispersal or persistence limitation (Stubbs & Wilson, 2004; Götzenberger et al., 2012). As the functional species pool method allows minimising the effect of environmental filtering, convergence at the broader scale for both stable and dynamical grasslands is likely caused by the selective persistence of certain phenotypes and non-random extinction and colonisation events.

4.2. Functional and taxonomic diversity in historical and current grasslands

During the last 90 years, the studied calcareous grasslands in northern Estonia have lost 90% of their area and nearly 30% of their characteristic plant populations (**I**), which corresponds closely to the predicted extinction debt of 40% for the better-preserved western Estonian alvar grasslands (Helm et al., 2006). Despite the loss of many habitat characteristic plant species, both functional and taxonomic diversity were higher in degraded remnants compared to functional and taxonomic diversity in 1930s. Unexpected increasing trend in species richness can be at least partly explained with the changed productivity and management regime of the sites. Calcareous grasslands are characterized by low productivity and quite extreme environmental conditions (thin soils, irregular droughts and floods), which limit the number of species able to survive harsh conditions (Helm, 2011). Due to indirect factors (e.g. inflow of nutrients through atmospheric nitrogen deposition or from neighbouring arable fields) and/or direct factors (e.g. applications of fertilizers), productivity of the sites has increased, but not yet to the extent that would reduce species richness (Fraser et al., 2014). Although abandonment of grazing has often decreased species richness (Aavik, et al., 2008), ceased grazing in these low productivity grasslands could have a positive effect on species richness, enabling the growth of taller, shade-tolerant species (Vandewalle et al., 2014; Neuenkamp et al., 2016). According to historical descriptions (Vilberg, 1927), the studied sites were grazed quite intensively and tended to have lower species richness compared to adjacent mown grasslands, indicating possible overgrazing.

Despite the increased taxonomic and functional richness, grassland integrity hasdecreased considerably, indicating the lowered quality of current alvars compared to historical communities (**III**). Increased proportion of derived species (i.e. species not characteristic to dry calcareous grasslands, but more typical of less disturbed and more productive open habitats, such as abandoned fields and cultural grasslands) and an accompanied reduced number of characteristic species (i.e. historically typical species at a given community) has occurred possibly due to eutrophication and cessation of grazing during the study period.

4.3. Losers and winners in changing grasslands

Despite the different approaches applied to determine species sensitivity to local extinctions, functional traits and habitat preferences characteristic of locally decreasing and more successful species led to similar results in papers **II**, **III**, and **IV**. As a general tendency, species with strategies allowing long-distance dispersal (indicated by lower seed weight, anemochorous seeds and lower terminal velocity of seeds) were more prone to local extinction (**II**, **III**, **IV**). Species that usually benefit from long-distance dispersal can be disadvantaged in contemporary grasslands. This tendency can be caused by decreased connectivity of habitat patches, hostile landscape matrices or unsuitable vegetation structure that increases the mortality of diaspores and restricts effective seed dispersal between semi-natural grassland sites, resulting in the collapse of metapopulation dynamics on which many well-dispersed species may depend (Maurer et al., 2003; Riba et al., 2009; Neuenkamp et al., 2016). Moreover, being myrmecohorous, autochorous or hemerochorous increased species' probability of being more vulnerable to changes in European grasslands (**IV**), indicating the difficulties also that specialized short-dispersing species face in fragmented landscapes (Vittoz & Engler, 2007). However, the loss of myrmechorous species can be related to the decline in ant species due to increased agricultural activities (De Bruyn, 1999) and urbanisation (Lach et al., 2010), while disrupted dispersal of hemerochorous species can be caused by reduced mowing or grazing. At the same time, species with unspecialized dispersal were rather benefitted by the changes (**IV**). Despite the lack of any special dispersal mechanisms or characteristics, these species tend to have relatively wide range sizes (Fitter & Peat, 1994), which suggests relatively good dispersal ability.

The trade-off between traits related to species dispersal (i.e. number of seeds, terminal velocity) and establishment (i.e. seed size; Kneitel & Chase, 2004) suggests that current conditions with high local competition for light and space benefit species with more successful local establishment ability (Westoby, 1998; Jakobsson & Eriksson, 2000; Moles & Westoby, 2004;). Species characterized by heavier seeds and higher terminal (**II**, **III**) were preferred in remnant grasslands in northern Estonia and grasslands across Europe (**IV**), indicating that not better dispersal ability but rather competitive advantage in more productive sites ensures species persistence (Soons & Heil, 2002).

The importance of competitive ability was further demonstrated by the result that species with competitive strategy, higher average height (> 0.4 m; **II**) and higher SLA had more likely increased their occurrence or abundance compared to species with other strategy types (**IV**), lower height or lower SLA (**II**, **III**, **IV**). Shorter species with lower SLA are probably outcompeted by taller species with higher SLA, which are adapted to more productive and less disturbed habitats (Walker & Preston, 2006; Van Calster et al., 2008). The decline of poor competitors in grasslands appears to be a general trend in Europe and it has been detected also in several earlier studies (e.g. Diekmann et al., 2014; Kana et al., 2015; Timmermann et al., 2015).

Species lacking clonal growth (**II**, **IV**) and persistent seedbank (**IV**) were more susceptible to local extinction, indicating their lower persistence ability compared to more successful species. Clonality is suggested to be particularly important for species persistence in disturbed and anthropogenically influenced habitats (Fahrig et al., 1994), but also in isolated and abandoned grasslands (Bruun, 2000; Piessens & Hermy, 2006; Johansson et al., 2011, but see Marini et al., 2012; Lindborg et al., 2012; Wesche et al., 2012), where it enables species to overcome long-lasting harsh periods. Persistent seed bank poses a similar advantage by providing a temporal rescue (Piessens et al., 2004). However, seedbank longevity had no effect on species extinction in calcareous grasslands (**II**, **III**), likely because unfavourable conditions have persisted in our studied habitats for more than half a century, thus the benefits of a persistent seed bank have already been exhausted (Dutoit & Alard, 1995). Unexpectedly, life span did not affect species' proneness to decrease in European grasslands, although short-lived species had higher probability for local extinction in severely fragmented grasslands, due to probably faster response to environmental changes (Fischer & Stöcklin, 1997, Purschke et al., 2012; **II**). Similarly, different pollen vectors had no effect on species local trend in European grasslands, although isolation and habitat loss have often been found to have a more negative effect on insect-pollinated species (Kolb & Diekmann, 2005), which could be further expected in the light of the drastic decline in the airborne insect biomass detected in European landscapes (more than 75% over 27 years) (Hallmann et al., 2017). In the northern Estonian study (**II**) self-pollinators were more threatened, likely due to inbreeding in highly fragmented habitats (Keller & Waller, 2002).

More successful species in European grasslands were facultatively associated with mycorrhizal fungi (i.e. mycorrhizal flexibility sensu Moora, 2014) (Smith & Read, 2008; Moora, 2014; **IV**), while non-mycorrhizal or obligatory mycorrhizal (i.e. inflexible) species had a tendency to be losers. Being flexible regarding mychorrizal symbiosis can give an advantage in conditions where it is not essential to have a symbiont, e.g. in the case of nutrient surplus. Thus, species that are able to control the mycorrhizal symbiosis can be better competitors in such conditions (Hempel et al., 2013; Moora, 2014). Additionally, species with mycorrhizal flexibility are characterized by wider niches and broader ecological requirements at the regional scale, likely due to their ability to tolerate and adapt to the changed environmental conditions (Hempel et al., 2013; Gerz et al., 2018).

Anthropogenic tolerance influenced species occurrence in European grasslands – urbanophobic species were more vulnerable to the changes compared to more tolerant species. Increasing urbanization and anthropogenic influence on different communities threatens numerous urbanophobic species, while the trend of urbanophilic species occurrence increases (Jandt et al., 2011; Laanisto et al., 2015).

Species habitat requirements were highly significant in determining species occurrence in highly degraded grasslands. Species with preference for lower

soil nitrogen content, lower soil reaction and lower temperature, but for higher light availability were more prone to extinction. This ubiquitous trend, recorded also in many earlier studies across Europe, is probably caused by decreased habitat quality either due to increased eutrophication or the lack of traditional management (e.g. Van Landuyt et al., 2008; Stevens et al., 2010) and has shifted plant communities toward compositions typical of high nitrogen availability conditions (e.g. Bobbink et al., 2010). Additionally, atmospheric nitrogen deposition is tightly connected with changes in soil chemistry and a decrease in soil reaction, leading to changes in vegetation (Horswill et al., 2008; Duprè et al., 2010; Stevens et al., 2010). Particularly strong negative effects on vegetation are encountered in acid grasslands and heaths (Van Landuyt et al., 2008; Maskell et al., 2010; Stevens et al., 2016), although calcareous grasslands are affected as well, despite their better buffering ability (Horswill et al., 2008; Van Den Berg et al., 2011). In agreement with previous results, species adapted to cooler conditions or higher elevations had a higher risk of decline (Newton et al. 2012; De Frenne et al. 2013), suggesting the possible effects of climate change and immigration of species with preferences for higher temperatures.

4.4. Implications for conservation and restoration

The year 2010 was the United Nations' International Year of Biodiversity and was predicted to be the culmination in the decline of biodiversity. However, a report by Butchart et al. (2010) and many others have revealed that the 2010 target was not met and the loss of biodiversity continues. The European Union has set an ambitious target to halt the loss of biodiversity by the year 2020 (EU Biodiversity Strategy to 2020). Among the other subtasks, a goal has been set to enhance restoration activities in degraded ecosystems where at least 15% of degraded ecosystems are to be restored by 2020 to enable the maintenance of ecosystems and their services and to prevent global biodiversity loss.

The results of this thesis highlighted in many ways the need for active conservation and restoration activities to preserve valuable semi-natural and natural grassland communities with high conservation importance (**II**, **III**, **IV**). Information on the differences in functional traits of locally extinct species and species that are still present in habitat remnants allowed us to distinguish which landscape and local environment factors are most crucial for the persistence of populations and which should be considered when designing restoration projects and developing appropriate management activities (**II**, **III**, **IV**). Together with species local extinctions, European grasslands have lost a unique part of their functional traits, which have not been fully replaced by new species, indicating the potential threat of losing important functions and services that grasslands offer (**IV**). Species that have shown larger declines over the past decades have to be taken into consideration when planning conservation measures in grasslands.

Strong convergence patterns in dispersal traits in former grasslands indicate probable dispersal limitation and lack or failure of some essential dispersal vectors (**I**). The same trend was detected in highly degraded semi-natural calcareous grasslands in Estonia, as well across European grasslands, where species with good dispersal ability (e.g. lower terminal velocity, lighter seeds) had a higher probability of local extinction (**II**, **III**, **IV**). Furthermore, species with shorter height, preference for lower soil productivity and higher light requirements were outcompeted in the taller vegetation under higher productivity conditions. My results indicate that decreased habitat connectivity and declined habitat quality are crucial drivers in determining local population extinction. According to results of papers **I**, **II**, **III**, **IV** and several earlier studies (e.g Van Landuyt et al., 2008; Stevens et al., 2010), the decreased quality of habitats is caused mainly by increased eutrophication or the lack of traditional management activities. In order to improve the conditions for long-term persistence of good dispersers, conservation activities need to focus both on improving remnant habitat quality for short, stress-tolerant grassland species and on restoring habitat connectivity to promote species dispersal between habitat patches. A large enough number of habitats in good condition and with good connectivity are needed to ensure effective dispersal.

Measures used for the management of grasslands to control the impact of nitrogen deposition include actions to mitigate eutrophication (e.g. by reducing competition for light and by removing nitrogen from the system) and to mitigate acidification (e.g. through liming) (Stevens et al., 2011). When the aim is to reduce competition for light and to remove nitrogen from the system, it may be essential to restore the traditional management activity, increase the cutting frequency or grazing intension, to remove biomass by cutting and gathering the hay, although these methods are not cost-effective nowadays. An alternative method for removing reactive nitrogen from soils is the addition of carbon either in the form of sucrose, sawdust, starch or cellulose. In this method the carbon:nitrogen ratio of soil increases, which in turn stimulates microbial communities to immobilize nitrogen in the soil, thus making it inaccessible to plants (Török et al., 2000; Eschen et al., 2007). However, the effect of carbon in reducing productivity and increasing species richness is doubtful. For example, the addition of carbon in the form of sucrose (1000 $g \cdot m^{-2} yr^{-1}$) in a mesophytic grassland in southeast Estonia efficiently decreased the above-ground biomass but did not result in much change in community composition after 10 years (Liira et al., 2012). Turf stripping and topsoil removal are the most dramatic method for the elimination of nutrients that have been used extensively in more degraded landscapes, e.g. in the Netherlands for the restoration of heathlands (De Dorland et al., 2005). The abovementioned methods are unsuitable for application at a larger scale (e.g. landscape scale) and are more appropriate for sites of targeted areas or high conservation value (Stevens et al., 2011). The only effective and sustainable method to reduce the impact of nitrogen is through the reduction of nitrogen emissions (Stevens et al., 2011). However, often the conservation and management actions provided in protected areas are

not enough to avoid further loss of habitat area and vegetation changes (Ridding et al., 2015).

The delayed response of many habitat characteristic species would give additional time to elaborate the most suitable conservation actions. Traits of locally extinct species can be used to identify species that constitute extinction debt in communities, where habitat loss or quality decrease has been less considerable, and where the extinction debt is still unpaid. Remarkably, we found that species which currently show a stable trend in European grasslands may become threatened in the future as their functional characteristics were in several cases more similar to losers than to winners (**IV**). The similarity of trends hints that despite a currently stable trend, these species are affected by the changing conditions and could at least partially decline in the future. Thus, many of the currently remaining species, both losers and stable, are likely to decline further in the near future under the continuing anthropogenic pressure on grassland habitats. This aspect needs to be taken into account in the conservation and restoration management of grasslands in order not to overestimate the habitat status.

Although young developing grasslands can be in their general appearance very similar to dry calcareous grasslands with long and regular management activity, assembly patterns and mechanisms operating behind developing and historical grasslands differ considerably (**I**). Thus, hoping for young and developing communities to become a new home for habitat specialists is limited.

Vegetation re-surveys provide valuable information on habitat change and to help to investigate mechanisms of species loss and colonization. It is highly important to conduct and report all vegetation analysis in a way that they would be fully repeatable in the future. Furthermore, in addition to vegetation data, information on environmental conditions would be highly valuable for future re-surveys. There is still a need for similar studies at larger scales and with more comprehensive data to assemble the findings from different regions and background conditions to draw conclusions on the general patterns and drivers governing the changes in European grassland ecosystems.

5. CONCLUSIONS

In this thesis, I summarised four papers focusing on the dynamics of grassland plant diversity and species composition in response to land-use change, extensive fragmentation and environmental degradation. I studied what drives the community assembly in grassland ecosystems at different spatial scales and used re-survey studies to detect directly which species suffer and benefit most under changing conditions in European grasslands.

The study revealed that grasslands with long and regular management were assembled differently from abandoned and young developing grasslands, but these differences became evident only at finer scales (**I**). Divergence patterns in grasslands are at least partly caused by long and moderate management history (e.g. grazing), which allows co-existence of functionally dissimilar species and niche differentiation. Species with more similar functional traits were filtered into local communities in dynamic habitats, indicating that exclusion of unsuitable phenotypes and poor competitors, as well as dispersal limitation, are the main mechanisms causing convergence patterns in dynamic grassland habitats. Individual trait analyses led to varying assembly patterns, suggesting that different characteristics are important for determining species co-occurrence patterns under diverse land-use scenarios. Irrespective of land-use history, convergence patterns became more prevalent with increasing scale, indicating that dispersal limitation and elimination of unsuitable phenotypes affect species assembly at broader scales.

Testing re-survey data in Estonian dry calcareous grasslands and grasslands across different parts of Europe allowed us to assess directly the changes in plant diversity following habitat change. Altered conditions have caused shifts – both declines and increases – in plant species occurrence and abundance, affecting probably the overall ecosystem functioning. Species composition differed in currently highly degraded dry calcareous grassland remnants compared to historical grasslands in good condition (**II**, **III**). Despite the local extinction of several characteristic species populations, total species richness and functional diversity of several life-history traits had increased in dry calcareous grassland remnants, where extinction debt was probably already paid. Increased diversity is caused by immigration of new species, characteristic to other types of habitats (**III**). Considering the declined habitat integrity, these calcareous grassland fragments have largely lost their conservation value as dry calcareous grasslands but can still contribute to local biodiversity conservation due to their high diversity (**III**).

Populations more susceptible to local extinctions after changes in land-use and environmental conditions were characterized by different life-history traits and habitat preferences compared to more successful species. Species with good dispersal ability, but poorer abilities for local persistence and competition are more susceptible to habitat loss and decreased habitat quality (**II**, **III**, **IV**). Decreasing species had lighter seeds, dispersal by wind or by ants, man or

explosive mechanisms, lower terminal velocity, lower height, lower SLA. Additionally, species more prone to local extinctions were without vegetative reproduction, urbanophobic, obligately mycorrhizal or nonmycorrhizal and had different environmental preferences (lower soil reaction, temperature and nitrogen content preferences, but higher preference for light availability). Traits characterizing locally extinct species can be used to identify species that constitute extinction debt in communities where habitat loss or quality decline has been less severe. Species sensitivity to local extinction was not affected by the intraspecific variability of the tested continuous traits related to competitive, dispersal and establishment abilities (**IV**). The life history traits and habitat preferences that were significantly related to species local extinctions suggest that changes in biotic and abiotic conditions due to inadequate management and eutrophication, fragmentation, urbanization and climate changes are the main drivers of change in European grasslands (**II**, **III**, **IV**). Beside species local extinctions, European grasslands have lost a unique part of their functional traits, which were not replaced by the new species in the communities. This demonstrates the potential threat of losing important functions that grasslands offer (**IV**).

The results of this thesis highlighted in many ways the need for active management and restoration activities to preserve valuable semi-natural and natural grassland communities with considerable conservation importance. Considering species functional traits, wiser decisions can be made to mitigate the further decline in biodiversity. Conservation measures have to focus on still common but at the same time threatened species.

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SUMMARY IN ESTONIAN

Niidutaimede mitmekesisuse dünaamika muutuvates maastikes

Elurikkuse pidev vähenemine on käesoleval sajandil ühiskonna üheks suurimaks väljakutseks. Looduslikele kooslustele asulate, põllumaade või istanduste rajamine, traditsioonilistest majandusvõtetest loobumine, väetamine, lämmastiku sissevool ja kliimamuutused on vaid mõned näited elurikkust viimase saja aasta jooksul oluliselt mõjutanud teguritest. Kunagiste laialdaselt levinud poollooduslike rohumaade pindala on mitmel pool Euroopas vähenenud isegi kuni 97% võrreldes nende liigirikaste koosluste ajaloolise levikuga. Lisaks on suur osa pool-looduslikest ja looduslikest niitudest nüüdseks tugevalt killustunud ja kahjustunud, millega on omakorda kaasnenud mitmete elupaigale iseloomulike (nn elupaigaspetsiifiliste) liikide populatsioonide seisundi oluline halvenemine või isegi lokaalne kadumine. Seoses taimepopulatsioonide aeglase dünaamikaga võib liikide reageering muutunud keskkonnatingimustele toimuda sageli viivitusega ning liikide lõplikuks kadumiseks killustunud kooslustest kuluda mitmeid aastakümneid või rohkemgi. Nähtust, kus liik on määratud kadumisele seoses minevikus toimunud sündmustega, nimetatakse väljasuremisvõlaks. Liikide hilinenud reageering raskendab arusaama killustumise ja elupaiga halvenemise mõjust. Väga keeruline on hinnata nende nähtuste lõplikke tagajärgi ökosüsteemide toimimisele ja inimeste heaolule. Väljasuremisvõlga on täheldatud väga erinevate organismirühmade, eelkõige aga elupaigaspetsiifiliste liikide puhul. Näiteks on Helm jt. (2006) Lääne-Eesti loopealsetel hinnanud väljasuremisvõla ulatust ja avastanud, et sealsete loopealsete pindala 70% vähenemisega võib kaasneda ligi 40% loopealsetele iseloomulike liikide kadumine juhul, kui väljasuremisvõlg on „makstud“. See tähendab umbes 20 liigi kadumist igalt looalalt. Kui väljasuremisvõla suurust on võimalik hinnata tänapäevase ja ajaloolise pindala muutuse kaudu, siis tunduvalt keerulisem on välja selgitada need liigid, mida lokaalne kadumine esmajoones ohustab.

Elupaiga pindala ja kvaliteedi vähenemisega ei pruugi alati kaasneda vaid liigirikkuse kadumine. Liigirikkuse vähenemist või suurenemist lokaalses või regionaalses skaalas mõjutab tasakaal väljasuremiste ja uute liikide saabumise vahel. Hoolimata mitmete elupaigaspetsiifiliste liikide lokaalsest kadumisest või ohtruse vähenemisest, on üldine liigirikkus pool-looduslikes kooslustes pärast traditsioonilistest majandusvõtetest loobumist mõnikord hoopiski tõusnud. Üldise liigirikkuse tõus majandamise lõppedes võib olla tingitud uute liikide lisandumisest, mida pidev majandamine varasemalt takistas ja millele muutunud tingimused just paremini sobivad. Koosluste liigilise koosseisu sarnasus algsele nn rikkumata kooslusele (kooslus enne ulatuslikku pindala vähenemist ja/või kvaliteedi langust) on siiski vähenenud ja looduskaitseline väärtus langenud spetsialistide vähenemise ja mittespetsiifiliste liikide sissetungi tõttu.

Maakasutuse muutustega seoses on muutused täheldatavad ka koosluse funktsionaalses koosseisus. Liikide vastus elupaiga seisundi muutustele sõltub suuresti liigi funktsionaalsetest (kasutatakse ka mõistet "elukäigu") tunnustest ja elupaiganõudlustest. Funktsionaalseteks nimetatakse organismi kohasust mõjutavaid morfoloogilisi, füsioloogilisi, struktuurseid, fenoloogilisi ja käitumuslikke tunnuseid. Kui uurimise all on koosluse pindalakao, killustumise ja kvaliteedi languse mõju elurikkusele, on oluline uurida levimise ja püsimisega seotud elukäigutunnuseid. Euroopa rohumaadel on seoses eutrofeerumise ja traditsiooniliste majandamisvõtete hääbumisega leitud, et parema konkurentsivõimega liigid on lokaalsele väljasuremisele maakasutuse muutuste korral vähem altimad võrreldes liikidega, mis on kohanenud pidevale häiringule ja koosluste väiksemale produktiivsusele. Killustunud elupaikades võib liigile tulla kasuks parem levimisvõime (kergemad ja paremini lenduvad seemned, tuullevi), mis annavad võimaluse vajadusel ühest elupaigalaigust teise levida. Samas seoses lõivsuhtega konkurentsi- ja levimisvõime vahel, võivad heade levimisomadustega liigid olla madala kvaliteediga elupaikades väljasuremisele siiski altimad, seda ka seetõttu, et hea levimisvõime korral on liigil suurem võimalus sattuda ebasobivasse keskkonda. Sageli on funktsionaalsetele tunnustele keskendunud töödes leitud üsna vastuolulisi tulemusi, mis võivad varieeruda nii uuritud tunnuste, koosluste kui kasutatud meetodite osas ning hoolimata intensiivsest uurimispanusest on liikide ning koosluste säilimise osas seoses elupaiga muutustega veel palju vastuseta küsimusi.

Oluliseks aspektiks taastamis- ja kaitsetegevuste väljatöötamisel on mõista, millised protsessid ja tegurid mõjutavad liikide kooseksisteerimise mustreid kooslustes enim. Funktsionaalsete tunnuste struktuur ja kooskasvavate liikide funktsionaalsete tunnuste väärtused võivad anda olulist informatsiooni liigilist koosseisu mõjutavate peamiste mehhanismide ja protsesside osas maakasutuse muutuste tagajärjel. Väiksemas skaalas kooskasvavad liigid võivad olla funktsionaalsete tunnuste osas üksteisele sarnasemad või erinevamad, kui võiks oletada suuremas skaalas leiduvate liikide juhusliku sisserände järgi. Võimalikult erinevate tunnustega liikide kooskasvamine viitab, et liikide esinemine koosluses on määratud eelkõige biootiliste interaktsioonide poolt (näiteks läbi konkurentsi limiteerivate ressursside – valgus ja toitained pärast). Sarnasemate tunnustega liikide kooskasvamine viitab aga eelkõige teatud keskkonnafiltrite, konkurentse väljatõrjumise või levimispiirangute olulisusele liigilise koosseisu kujunemisel.

Maakasutuse näitajad, nagu elupaiga vanus, selle majandamise järjepidevus ja intensiivsus, mõjutavad tugevalt rohumaade liigilist ja funktsionaalset koosseisu. Arvukatest publikatsioonidest hoolimata on senini teadmata, mil määral olenevad koosluste kujunemine ja seal toimuvad protsessid maakasutuse ajaloost.

Minu doktoritöö eesmärgiks oli uurida niiduliikide mitmekesisuse dünaamikat ja liigilise koosseisu muutusi seoses elupaiga pindala vähenemise, kvaliteedi languse ja muutunud keskkonnatingimustega. Esiteks soovisin välja selgitada, missugused protsessid mõjutavad koosluste kokkupanekut erineva maakasutuse

ajalooga niidukooslustes. Täpsemalt soovisin teada saada, kas regulaarselt ja pikka aega majandatud niidukooslused on võrreldes dünaamiliste kooslustega (nagu kinnikasvanud endised looniidud või kujunevad niidukooslused) erinevalt „kokku pandud“ ja millised protsessid (levimispiirangud, abiootilised tingimused, biootilised interaktsioonid) on kõige olulisemad niitude liigilise koosseisu kujunemisel erinevates ruumiskaalades (**I**). Teiseks võrdlesin liigilist koosseisu nüüdseks tugevalt kahjustunud ja killustunud Põhja-Eesti kuivadel looniidujäänukitel samade alade ajalooliste liiginimekirjadega (**II**, **III**). Soovisin välja selgitada, kas liigirikkus, funktsionaalne mitmekesisus ja koosluste iseloomulikkus on 90 aasta jooksul vähenenud võrreldes G. Vilbergi poolt 1918.–1923. aastatel kogutud andmetega. Samuti uurisin, milliste funktsionaalsete tunnuste ja elupaiganõudlustega on liigid, millel on vaadeldud ajavahemikus olnud suurem tõenäosus lokaalseks väljasuremiseks või mis on muutuste järgselt alale jõudnud ja seal oma ohtrust suurendanud (**II**, **III**). Põhja-Eesti loopealsetel suurema kadumisriskiga liigid võimaldasid hinnata ka seda, missuguste funktsionaalsete tunnustega liigid moodustavad tõenäoliselt väljasuremisvõla pool-looduslikes kooslustes teistes Eesti piirkondades, kus muutused ei ole olnud veel nii suured (**II**). Järgnevalt soovisin välja selgitada, millised erinevused kehtivad „kadujate“ ja „võitjate“ osas Euroopa rohumaadel (**IV**). Kahekümne kahe ajalooliste ja tänapäevaste liiginimekirjadega töö analüüsimisega soovisin leida vastuse küsimustele, milliste tunnuste ja elupaiganõudlustega liike ohustab Euroopa niitudel lokaalne väljasuremine enim ning kas liigi edukus sõltub ka elukäigutunnuste liigisisesest varieeruvusest (**IV**). Lisaks soovisin välja selgitada, kas Euroopa niidud on seoses liikide lokaalse väljasuremisega kaotanud eriomase osa funktsionaalsetest tunnustest ja kas liigilise koosseisu muutusetega on kaasnemas muutused rohumaaökosüsteemide talitluses (**IV**). Viimaseks doktoritöö eesmärgiks oli oma tulemustele (**I**, **II**, **III**, **IV**) tuginedes pakkuda välja soovitusi väärtuslike niidukoosluste elurikkuse säilitamiseks, kaitseks ja taastamiseks.

Pikaajalise majandamise olulisuse väljaselgitamiseks liikide kooseksisteerimisele valisime Saare- ja Muhumaal 35 niidukompleksi, kus olid lähestikku esindatud nii regulaarselt hooldatud loopealne, metsastunud või majandamise lakkamise tõttu kinnikasvanud endine loopealne ning alles kujunemas niidukooslus (teeveer, endine põlluala), kus oli hooldamine alles hiljuti alanud (**I**). Igas niidukompleksis kirjeldati erineva majandamisajalooga elupaigas soontaimede ohtrus 2 × 2 m ruudul ja 50 m raadiuses ümber ruudu (nn. lokaalkooslus). Iga liigi osas oli vaatluse all kaheksa funktsionaalset tunnust, mille väärtused otsiti erinevatest andmebaasidest. Liigilise koosseisu mustreid ja neid mõjutavaid mehhanisme uurisime igas niidutüübis kahes skaalas: 1) 2 × 2 m ruudus võrreldes ruutu ümbritseva 50 m raadiuse kooslusega ning 2) lokaalses koosluses võrreldes antud niidutüübi 35 alal leiduvate liikidega. Selgitamaks välja, millised tunnused määravad liigi sattumise lokaalsest kooslusest ruudule, arvutasime erineva majandamisega niitudel kooskasvavate liikide kaalutud keskmised ruudul ja võrdlesime neid kaalutud keskmistega liikidel, mis leidusid lokaalses skaalas, aga mitte ruudul.

Kui esimeses töös uurisime liigilise koosseisu dünaamikaid kasutades selleks sama ajahetke, aga erinevaid ruumipunkte, siis järgnevates töödes (**II**, **III**, **IV**) oli meil võimalik uurida taksonoomilise ja funktsionaalse liigirikkuse muutusi erinevates ajahetkedes, kasutades selleks ajaloolisi ja tänaseid liiginimekirju. Erineva ajahetke liiginimekirjade võrdlemine võimaldas uurida, milliste funktsionaalsete tunnustega ja elupaiganõudlustega liigid on oma ohtruses vähenenud või kadunud, millised suurenenud või juurde tulnud (**II**, **III**, **IV**), millised jäänud stabiilseks (**IV**). Elupaigaspetsiifiliste liikide suhtelise muutuse abil oli võimalik hinnata koosluse iseloomulikkuse muutusi kahe ajahetke võrdluses (**III**).

Kolmekümne viie erineva maakasutuse ajalooga niidukompleksi uurimine Saaremaal näitas, et kuigi regulaarselt hooldatud ja liigirikkad loopealsed on teeveertel ja endistel põllumaadel kujunevate noorte kooslustega pealtnäha üsna sarnased, kasvavad ajaloolistes liigirikastes kooslustes kõrvuti erinevate tunnustega liigid, kui oleks oodanud suuremas skaalas leiduvate liikide põhjal (**I**). Samas on alles kujunevates noortes kooslustes ja metsastuvatel endistel loopealsetel väikeses skaalas koos kasvamas pigem sarnaste tunnustega liigid. Erinevate tunnustega liikide koosesinemine ajaloolistel niitudel viitab pikaajaliste majandamistegevuste olulisusele elurikkuse kujunemisel. Sarnasemate funktsionaalsete tunnustega liikide koosesinemine alles kujunevatel ja kinnikasvavatel niitudel näitab, et peamisteks liigilist koosseisu mõjutavateks mehhanismideks dünaamilistes kooslustes on ebasobivate fenotüüpide kadumine ja konkurents ressursside pärast. Kinnikasvavatel niitudel leidsime osade tunnuste korral, et kõrvuti kasvasid pigem erinevate tunnustega liigid (**I**). See tulemus viitab, et antud kooslustes võib väljasuremisvõlg olla veel maksmata. Suuremas skaalas domineerisid kõigis uuritud niidukooslustes olenemata maakasutuse ajaloost sarnasemate tunnustega liigid, mis viitab levimispiirangute ja ebasobivate fenotüüpide eemaldamise olulisusele koosluste kujunemisel. Meie töö näitab selgelt, et maakasutuse ajalugu mõjutab oluliselt seda, millised protsessid koosluses toimuvad ja millised liigid koos kasvavad.

Uuritud Põhja-Eesti looniitude pindala on viimase 90 aasta jooksul vähenenud 90% ja lokaalselt oli välja surnud 30% loopealsetele iseloomulikest liikidest (**II**). Suurema lokaalse väljasuremisriskiga olid liigid, mis on ühe- ja kaheaastased, isetolmlejad, seemnelise levikuga ja vegetatiivse paljunemiseta, väikese seemneproduktsiooniga, madalakasvulised, väiksemat mullaproduktiivsust eelistavad või suure valgusnõudlusega liigid. See tulemus näitab, et pindalakaole ja elupaikade kahjustumisele on altimad pigem liigid, mis on nõrga konkurentsivõimega ning piiratud võimega taluda muutusi elupaikade biootilistes ja abiootilistes tingimustes. Lisaks olid lokaalselt väljasurnud populatsioonidele iseloomulikud kerged ja hea lenduvusega seemned ning tuullevi, mis näitab, et tugevalt killustunud maastikes ei ole hea levimisvõime liigile kasulik ning antud maastikes on olulisemad pigem tunnused, mis soosivad püsimist olemasolevas kasvukohas. Funktsionaalsed tunnused ja elupaiganõudlused, mis olid iseloomulikud Põhja-Eesti looniitudel lokaalselt kadunud populatsioonidele, võivad anda olulist infot nende liikide osas, mida võib lokaalne

kadumine ohustada looniitudel, kus pindala ja keskkonnatingimuste muutused ei ole nii märkimisväärsed kui Põhja-Eestis, näiteks Eesti lääneosa ja saarte looaladel, kus väljasuremisvõlg on veel maksmata. Hoolimata märkimisväärsetest langustrendidest loopealsetele iseloomulike liikide mitmekesisuses, oli uuritud alade üldine liigirikkus ja osade tunnuste funktsionaalne mitmekesisus oluliselt suurenenud, tõenäoliselt seoses konkurentsivõimelisemate ja toitainerikkamaid tingimusi eelistavate pärismaiste liikide levikuga (**III**). Loopealsetele karakteersete liikide lokaalse kadumise ja muudele kasvukohatüüpidele iseloomulike liikide lisandumisega seoses oli aga vähenenud koosluste iseloomulikkus ehk elupaikade liigilise koosseisu sarnasus ajaloolistele heas korras looklooslustele.

Euroopa niitudelt 30 kuni 300 aasta tagant kogutud ajalooliste ja tänapäevaste liigiandmete võrdlemisel leidsime, et ligi 3000 liigivaatlusest olid lokaalselt kadunud 466 populatsiooni, 570 oli vähenenud ohtrusega, 682 stabiilse ja 639 suurenenud ohtrusega ning lisandunud oli 574 uut populatsiooni (**IV**). Sarnaselt Põhja-Eesti lookooslustele olid suurema tõenäosusega niitudelt kadunud hea levimisvõime ja nõrgemate konkurentsi- ning püsimisomadustega liigid. Erineva muutustrendiga liikide tunnuste analüüs näitas, et lokaalselt väljasurnud liigid olid oma tunnustelt võrreldes stabiilsete liikidega iselaadsemad. Tunnuste liigisisene varieeruvus ei omanud liigi kadumises või püsimises rolli. Liigi kadumist või püsimist oluliselt mõjutanud tunnuste põhjal võib oletada, et peamisteks teguriteks liigilise koosseisu muutuste taga on Euroopa rohumaade kvaliteedi langus seoses eutrofeerumise ja muutunud valgustingimustega, suurenenud elupaikade isolatsioon, linnastumine ja kliimamuutused. Käimasolevate protsesside leevendamine on hädavajalik nimetatud muutustele tundlikumate liikide säilimiseks Euroopa rohumaadel.

Taimestiku korduvanalüüsid on äärmiselt vajalikud koosluste muutuste uurimisel ja võivad anda väärtuslikku infot liikide kadumiste ja saabumiste osas. Muutuste väljaselgitamiseks peavad uuringud olema tehtud sellisel tasemel, et neid oleks tulevikus võimalik korrata. Lisaks taimkatte andmetele, oleks uuringutes vajalik kajastada ka keskkonnaparameetreid. Teades liikide tunnuseid, saame teha palju targemaid looduskaitselisi otsuseid elurikkuse kaitseks, suunates tähelepanu veel laialt levinud või alles hiljuti laialt levinud liikidele, mis on muutuste tõttu enim ohustatud.

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PUBLICATIONS

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Education:

2008–	University of Tartu, PhD candidate in botany and ecology
2005–2007	University of Tartu, MSc in environmental technology
2001–2005	University of Tartu, BSc in environmental technology, *cum laude*
1990–2001	Saaremaa's Co-ed. Gymnasium, class of mathematics and physics

Language skills:
Estonian (mother tongue), English (fluent), Russian (basic), Spanish (basic)

Institution and position held:

2018–	Saaremaa Municipality, nature conservation specialist
2017–	Tallinn University of Technology, Centre for Blue Economy, lecturer
2014	University of Tartu, Institute of Ecology and Earth Sciences, specialist
2008–2010	University of Tartu, assistant works
2011–2012	Archimedes Foundation, student research project supervisor
2007–2012	Archimedes Foundation, Environment National Contact Point for FP7
2006–2005	University of Tartu, project manager in free air humidity manipulation experiment (FAHM)
2006–2010	Archimedes Foundation, assistant of science popularization unit
2005	University of Tartu, technician

Research interests:
Landscape history, the effects of human-induced habitat fragmentation and following changes in biodiversity, drivers of high small-scale plant species richness, taxonomic and functional diversity in degraded landscapes, conservation and restoration of semi-natural grasslands.

Publications:

Saar, **L**., Takkis, K., Laanisto, L., Carmona, C.P., Kasari, L., Hallikma, T., Pärtel, M., & Helm, A. Losers and winners in European grasslands: a functional analysis of temporal trends of vascular plants. *Manuscript*

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Conference presentations:

Saar, **L**., Takkis, K., Laanisto, L., Kasari, L., Hallikma, T., Pärtel, M., Helm, A. Winners and losers in European grasslands: a functional analysis of large-scale trends of vascular plants. Nordic Oikos conference, 20–22 February 2018, Trondheim, Norway. *Poster presentation.*

Saar, **L**., Takkis, K., Helm, A. Plant extinctions and colonizations in European grasslands due to loss of habitat area and quality: a meta-analysis. International Biogeography Society 7th Biennial Meeting. 8–12 January 2015, Bayreuth, Germany. *Poster presentation.*

Saar, **L.,** Takkis, K., Helm, A. Plant extinctions and colonizations in European grasslands due to loss of habitat area and quality: a meta-analysis. 57th

Symposium of the International Association for Vegetation Science (IAVS), 1–5 September 2014, Perth, Australia. *Oral presentation.*

Saar, **L**., de Bello, F., Pärtel, M., Helm, A. Functional diversity and habitat filtering in stable and dynamic grassland communities. 26th Conference of the Plant Population Biology Section of the Ecological Society of Germany, Austria and Switzerland (GfÖ), 9–11 May 2013, Tartu, Estonia. *Poster presentation.*

Saar, **L**., de Bello, F., Pärtel, M., Helm, A. Trait filtering in stable and dynamic grassland communities. 56th Symposium of the International Association for Vegetation Science (IAVS), 26–30 June 2013, Tartu, Estonia. *Poster presentation*.

Saar, **L**., Szava-Kovats, R., Pärtel, M., Takkis, K., Helm, A. Larger species pools result in more specialist species in degraded habitats. 12th European Ecological Federation Congress.Euroopa Ökoloogiaföderatsiooni 12. kongress. 25–29 September 2011, Ávila, Spain. *Poster presentation.*

Saar, **L**., Pärtel, M., Takkis, K., Helm, A. Strategies of plants in fragmented grasslands: to endure or escape? Frontiers in Historical Ecology, 30 August–2 September 2011, Birmensdorf, Switzerland. *Poster presentation*.

Saar, **L**., Szava, R.-K., Pärtel, M., Takkis, K., Helm, A. Dynamics of Plant Species Richness in Calcareous Grasslands: Effects of Abandonment and Destruction. 24th Annual Conference of the Plant Population Biology Section of the Ecological Society of Germany, Switzerland and Austria (GfÖ), 2–4 June 2011, Oxford, England. *Poster presentation.*

Saar, **L**., Takkis, K., Pärtel, M., Helm, A. Locally extinct species shed light on the future of grassland biodiversity. International doctoral student's conference, 12–13 May 2011, Tartu, Estonia. *Poster presentation.*

Saar, **L**., Helm, A., Takkis, K., Pärtel, M. Species traits related to local extinctions in fragmented grasslands. 23th Conference-Expedition of the Baltic Botanists, 19–22 July 2010, Haapsalu, Estonia. *Poster presentation.*

Saar, **L**., Helm, A., Takkis, K., Pärtel, M. (2009). Species traits related to local extinctions in fragmented grasslands. 52th Symposium of the International Association for Vegetation Science (IAVS), 30 May–4 June 2009, Chania, Greece. *Poster presentation.*

Honours & awards

2011, 2014	Doctoral School of Earth Sciences and Ecology foreign visits scholarships
2010, 2011	Archimedes, DoRa T8 stipends "Participation of Young Researchers in the International Circulation of Knowledge"
2011	Archimedes, DoraT6 scholarship for visiting foreign lab
2009, 2010	Archimedes, Kristjan Jaak foreign visits scholarship
2005	Estonian National Contest for Young Scientists at university level, II Prize for BA thesis
2005	Scholarship of Johann von Luce hand out by the Union of local governments of Saaremaa

2003	14th European Union Contest for Young Scientists special award – taking part in research activities in Svålbard in Arctic region

Courses attended:

2015	International Biogeography society 7th biennial conference workshop "Towards the 'next generation' of species distribution modeling: emerging themes and methods", 8th January, University of Bayreuth, Germany
2011	Doctoral School of Earth Sciences and Ecology's Expedition to Iceland
2010	The Fifth ALTER-Net Summer School "Biodiversity and Ecosystem Services", 5–14 September, Peyresq, France
2009	PhD-course "A landscape approach to conservation" in 4–8 May, Stockholm University

R&D related managerial and administrative work

2014−	Field trips organizer of Environmental programs of Saare county
2014−	Member of the evaluation board of National Contest for Young Scientists
2010	Organizer of the Biodiversity Day of the GEO international magazine in Tartu, Estonia
2010	Organizer of the International training for scientists of food and agriculture, Tallinn, Estonia
2010−2011	Co-organizer of Biodiversity contest for school children "Our nature reserve", Tartu (2010), Aegna (2011), Estonia
2008−2016	Reviewer in Science Days organized by Saaremaa´s Co-ed. Gymnasium
2008	Moderator in Annual Conference of Students Scientific Association, Tallinn, Estonia
2007	Evaluator in the project "Our ecological house", Tartu, Estonia
2007	Organizer of Science Popularization Conference "Innovation Circus", Riga, Latvia
2006−	Member of the Estonian Green Movement-FoE
2006−2013	Reviewer of national contest for young scientists in nature field

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Töökogemus:

2018– Saaremaa vallavalitsus, looduskaitse peaspetsialist
2017– Tallinna Tehnikaülikool, Kuressaare Kolledž, lektor
2015–2016 Lääne-Saare vallavalitsus, keskkonnapeaspetsialist
2014– Keskkonnaprogrammide läbiviija Saaremaa Ühisgümnaasiumi Keskkonnahariduskeskuse projektis "Saare maakonna õpilaste keskkonnahariduslikud programmid"
2014– Õpilaste teadustööde riikliku konkursi hindamiskomisjoni liige
2014 Tartu Ülikool, loodus- ja tehnoloogiateaduskond, Ökoloogia- ja Maateaduste Instituut, spetsialist
2010 Rahvusvahelise GEO ajakirja Elurikkuse päeva korraldaja, Tartu, Eesti
2008–2010 Tartu Ülikool, preparaator
2008–2016 Saaremaa Ühisgümnaasiumi Miniteadupäevade superviisor
2008−2008 Õpilaste Teadusliku Ühingu aastakonverentsi moderaator, Tallinn, Eesti
2007–2012 Sihtasutus Archimedes, 7. raamprogrammi keskkonna valdkonna konsultant
2007 Teadust populariseeriva konverentsi "Innovation Circus" korraldaja, Läti, Riia

2006−2013	Õpilaste teadustööde riiklikule konkursile esitatud loodusvaldkonna tööde retsensent
2006	Tartu Ülikool, projektijuht Metsaökosüsteemi õhuniiskusega manipuleerimise eksperimendis (FAHM)
2006–2010	Sihtasutus Archimedes, Teaduse populariseerimise üksuse assistent
2005	Tartu Ülikool, loodus- ja tehnoloogiateaduskond, Tartu Ülikooli ökoloogia- ja maateaduste instituut, taimeökoloogia õppetool; tehnik

Peamised uurimisvaldkonnad:
Maastiku ajalugu, inimtegevuse poolt põhjustatud elupaikade killustumine ning elurikkuse muutused, liigirikkust mõjutavad tegurid erinevates ruumiskaalades, degradeerunud koosluste taksonoomiline ja funktsionaalne mitmekesisus, poollooduslike koosluste kaitse ja taastamine

Publikatsioonid:

Saar, **L**., Takkis, K, Laanisto, L., Carmona, C.P., Kasari, L., Hallikma, T., Pärtel, M., & Helm, A. Losers and winners in European grasslands: a functional analysis of temporal trends of vascular plants. *Manuscript*

Van Geel, M., Jacquemyn, H., Plue, J., **Saar**, **L**., Kasari, L., Peeters, G., Acker, K., Honnay, O., & Ceulemans, T. (2017) Abiotic rather than biotic filtering shapes the arbuscular mycorrhizal fungal communities of European seminatural grasslands. *New Phytologist*, aktsepteeritud avaldamiseks

Saar, **L**., de Bello, F., Pärtel, M., & Helm, A. (2017) Trait assembly in grasslands depends on habitat history and spatial scale. *Oecologia*, **184**, 1–12.

Kasari, L., **Saar**, **L**., de Bello, F., Takkis, K., & Helm, A. (2016) Hybrid ecosystems can contribute to local biodiversity conservation. *Biodiversity and Conservation*, **25**, 3023–3041.

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Gazol, A., Tamme, R., Takkis, K., Kasari, L., **Saar**, **L**., Helm, A., & Pärtel, M. (2012) Landscape-and small-scale determinants of grassland species diversity: direct and indirect influences. *Ecography*, **35**, 944–951.

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Saar, **L**.,Takkis, K., Helm, A. Plant extinctions and colonizations in European grasslands due to loss of habitat area and quality: a meta-analysis. Rahvusvahelise biogeograafide ühenduse 7. konverents. 8.–12. jaanuar 2015, Bayreuth, Saksamaa. *Posterettekanne.*

Saar, **L**., Takkis, K., Helm, A. Plant extinctions and colonizations in European grasslands due to loss of habitat area and quality: a meta-analysis. Rahvusvahelise Taimkatteassotsiatsiooni (IAVS) 57. sümpoosion, 1.–5. september 2014, Perth, Austraalia. *Suuline ettekanne.*

Saar, **L**., de Bello, F., Pärtel, M., Helm, A. Functional diversity and habitat filtering in stable and dynamic grassland communities. Saksamaa, Austria ja Šveitsi Ökoloogiaühingu (GfÖ) Taimede populatsioonibioloogia sektsiooni 26. konverents, 9.–11. mai 2013, Tartu, Eesti. *Posterettekanne.*

Saar, **L**., de Bello, F., Pärtel, M., Helm, A. Trait filtering in stable and dynamic grassland communities. Rahvusvahelise Taimkatteassotsiatsiooni (IAVS) 56. sümpoosion, 26.–30. juuni 2013, Tartu, Eesti. *Posterettekanne*.

Saar, **L**., Szava-Kovats, R., Pärtel, M., Takkis, K. Helm, A. Larger species pools result in more specialist species in degraded habitats. Euroopa Ökoloogia-föderatsiooni 12. kongress. 25.–29. september 2011, Ávila, Hispaania. *Posterettekanne.*

Saar, **L**., Pärtel, M., Takkis, K., Helm, A. Strategies of plants in fragmented grasslands: to endure or escape? Ajaloolaste ja ökoloogide ühiskonverents, 30. august–2. september 2011, Birmensdorf, Šveits. *Posterettekanne*.

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Saar, **L**., Takkis, K., Pärtel, M., Helm, A. Locally extinct species shed light on the future of grassland biodiversity. Rahvusvaheline doktorantide konverents. 12.–13. mai 2011, Tartu, Eesti. *Posterettekanne.*

Saar, **L**., Helm, A., Takkis, K., Pärtel, M. Species traits related to local extinctions in fragmented grasslands. Balti botaanikute XXIII konverents-ekspeditsioon, 19.–22. juuli 2010, Haapsalu, Eesti. *Posterettekanne.*

Saar, **L**., Helm, A., Takkis, K., Pärtel, M. Species traits related to local extinctions in fragmented grasslands. Rahvusvahelise Taimkatteassotsiatsiooni (IAVS) 52. sümpoosion, 30. mai–4. juuni 2009, Chania, Kreeka. *Posterettekanne.*

Saadud tunnustused, uurimistoetused ja stipendiumid

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2005	Saaremaa Omavalitsuste Liidu poolt välja antav Johann von Luce nimeline stipendium
2003	14. Euroopa Liidu Noorte Teadlaste konkursi eripreemia – osalemine teadusuuringutes Svålbardis, Arktikas

Erialane enesetäiendus:

2015	Rahvusvahelise biogeograafide ühenduse 7. konverentsi seminar "Liikide leviku modellerimise suundumused, teemad ja meetodid", 8. jaanuar, Bayreuth'i Ülikool, Saksamaa
2011	Maateaduste ja ökoloogia doktorikooli kompleksekspeditsioon Islandile
2010	5. ALTER-Net suvekool "Elurikkus ja ökosüsteemi teenused", 5.–14. september, Peyresq, Prantsusmaa
2009	Doktorantide kursus "Maastikuskaalaline lähenemine looduskaitsele", 4.–8. mai, Stockholmi Ülikool, Rootsi

Muu teaduslik organisatsiooniline ja erialane tegevus

2014−	Keskkonnaprogrammide läbiviija Saaremaa Ühisgümnaasiumi Keskkonna-hariduskeskuse projektis "Saare maakonna õpilaste keskkonnahariduslikud programmid"
2014−	Õpilaste teadustööde riiklikule konkursi hindamiskomisjoni liige
2010	Üleriigilise õpilastele ja teadlastele suunatud ajakirja GEO Elurikkuse päev peakorraldaja, Tartu, Eesti
2010	Rahvusvahelise koolituse peakorraldaja toidu- ja põllumajanduse valdkonna teadlastele 7. raamprogrammi projektikonkurssidel edukaks osalemiseks, Tallinn, Eesti
2010−2011	Elurikkuse võistlusmängu "Meie oma kaitseala" kaasorganiseerija, Tartu (2010), Aegna (2011), Eesti
2009–2010	Üleriigilise keskkonna valdkonna uurimistööde konkursi retsensent
2008−2016	Saaremaa Ühisgümnaasiumi Miniteadupäevade superviisor
2006−	Eesti Roheline Liikumise liige
2008	Õpilaste Teadusliku Ühingu aastakonverentsi moderaator, Tallinn, Eesti
2007	Tartu Keskkonnahariduse keskuse, Eestimaa Looduse Fondi ja Tartu Tamme Gümnaasiumi ühisprojekt – "Meie oma ökomaja" – hindamiskomisjoni liige

2007	Teadust populariseeriva ürituse "*Innovation Circus*" korraldaja, Riia, Läti
2006−2013	Õpilaste teadustööde riiklikule konkursi loodusvaldkonna tööde retsensent

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